THE ORDER MYRTALES: CIRCUMSCRIPTION, VARIATION, AND RELATIONSHIPS¹

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ABSTRACT

The Myrtales are one of the least controversial orders as regards circumscription and characterization. The core families are Onagraceae, Trapaceae, Lythraceae, Oliniaceae, Combretaceae, Alzateaceae, Rhynchocalycaceae, Penaeaceae, Crypteroniaceae, Melastomataceae, Memecylaceae, Psiloxylaceae, Heteropyxidaceae, and Myrtaceae. Psiloxylaceae-Heteropyxidaceae-Myrtaceae and Onagraceae form two somewhat peripheral groups within the order. Alzateaceae and Rhynchocalycaceae are newly recognized at the familial level. Punicaceae and Sonneratiaceae are included in Lythraceae. Crypteroniaceae and Memecylaceae could be included in Melastomataceae and Psiloxylaceae and Heteropyxidaceae in Myrtaceae. Lecythidaceae, Haloragaceae, Rhizophoraceae, and Thymelaeaceae are excluded from Myrtales. Arguments pro and con for this are given. The distribution of a number of attributes in the aforementioned families are discussed, and some distributions are illustrated diagrammatically. These attributes involve wood anatomy, foliar sclereids, phyllotaxy, stipular structures, merous conditions of perianth, inferior versus superior ovary placement, floral tube, pleiomery and developmental succession of stamens, anther connectives, pollen pseudocolpi, embryology, seed coat structure, chromosome numbers, chemistry, etc. Other families that have been associated with Myrtales are also considered. The Myrtales show affinities to Rosales, and fewer ones to Gentianales, Cornales, and possibly Theales.

CIRCUMSCRIPTION OF MYRTALES IN SOME CURRENT SYSTEMS OF CLASSIFICATION

The historical background of the order Myrtales will not be outlined here. We shall restrict ourselves to the circumscription of the order in the following classifications: Emberger (1960), Melchior (1964), Soó (1967), Hutchinson (1926, 1959, 1973), Thorne (1968, 1976, 1981), Cronquist (1968, 1981), Takhtajan (1969, 1980), Stebbins (1974), Dahlgren (1975a, 1980a), and Briggs and Johnson (1979).

Emberger (1960) included in this order: Lythraceae, Crypteroniaceae, Heteropyxidaceae, Sonneratiaceae, Punicaceae, Rhizophoraceae, Lecythidaceae, Combretaceae, Myrtaceae, Melastomataceae, Onagraceae, Trapaceae ("Hydrocaryaceae"), Haloragaceae ("Halorrhagidaceae"), and Gunneraceae, and, as annex families, added Hippuridaceae, Callitrichaceae, and Dialypetalanthaceae. Penaeaceae and Oliniaceae were placed in the adjacent order Thymelaeales,

which also included Thymelaeaceae, Geissolomataceae, and Elaeagnaceae.

This wide circumscription may be taken as a relevant starting point in this presentation, as here we have the essential scope of the order in a very wide sense. The general tendency has been to include Penaeaceae and Oliniaceae in Myrtales and to exclude Hippuridaceae and Gunneraceae (in as much as these are segregated from Haloragaceae), and also to exclude Lecythidaceae, Rhizophoraceae, and Haloragaceae sensu stricto. Dialypetalanthaceae have sometimes been very loosely attached to the order. Trapaceae are usually included in Myrtales and Heteropyxidaceae have usually been included in Myrtaceae, whereas, Psiloxylaceae are a recent addition to the Myrtaceae. Other later systems usually do not deviate greatly from this pattern.

In Melchior's (1964) edition of Engler's "Syllabus der Pflanzenfamilien," the following families are included in the order: Lythraceae, Trapaceae, Crypteroniaceae, Myrtaceae (incl.

The present summary presentation of Myrtales would not have been made without the encouragement from Dr. Peter H. Raven and all the contacts communicated by him. Numerous specialists in different fields for taxa within and without Myrtales have generously contributed information. Their contributions are acknowledged in the above text with the discrete remark, "personal communication." In particular, we wish to acknowledge ample first hand information from P. Baas, B. Briggs, S. A. Graham, A. Graham, L. Johnson, P. Raven, H. Tobe, C. A. Stace, and G. J. C. M. van Vliet. P. Raven, L. A. S. Johnson, B. Briggs, and R. Schmid have kindly read our manuscript and suggested many useful improvements and new data.

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Heteropyxidaceae), Dialypetalanthaceae, Sonneratiaceae, Punicaceae, Lecythidaceae, Melastomataceae, Rhizophoraceae, Combretaceae, Onagraceae, Oliniaceae, Haloragaceae (incl. Gunneraceae), and Theligonaceae, and in separate suborders Hippuridaceae and Cynomoriaceae. Inclusion of the last-mentioned familiy has gained no support. Penaeaceae, as in Emberger's (1960) classification, were placed in Thymelaeales, as were also Geissolomataceae, Dichapetalaceae, and Elaeagnaceae.

Soó (1967, 1975) subdivided his order Myrtales into three suborders: Myrtineae, with Combretaceae, Melastomataceae, Myrtaceae, Oliniaceae, Punicaceae, Sonneratiaceae, Lecythidaceae, and Rhizophoraceae; Lythrineae, with Lythraceae, Onagraceae, and Trapaceae; and Haloragineae, with Haloragaceae, Gunneraceae, and Hippuridaceae. Crypteroniaceae were omitted, and Penaeaceae were included in Thymelaeales.

Hutchinson (1926) in the first edition of his "Families of Flowering Plants" placed the families Lythraceae, Crypteroniaceae, Sonneratiaceae, Punicaceae, Oliniaceae, Onagraceae, Haloragaceae (including Gunnera and Hippuris), and Callitrichaceae in a separate order Lythrales; and Myrtaceae, Lecythidaceae, Melastomataceae, Combretaceae, and Rhizophoraceae in another order, Myrtales. These orders were at least partly distinguished by being chiefly herbaceous or chiefly woody, respectively, although this distinction had to involve many exceptions.

In the second edition of the same work (Hutchinson, 1959), with the same basic principle of division, the chiefly herbaceous Lythrales were restricted to Lythraceae, Onagraceae, Trapaceae, Haloragaceae, and Callitrichaceae; whereas the chiefly woody Myrtales included Myrtaceae, Lecythidaceae, Rhizophoraceae, Sonneratiaceae, Punicaceae, Combretaceae, and Melastomataceae. Crypteroniaceae and Oliniaceae in that edition were placed in Cunoniales and Penaeaceae in Thymelaeales. It is obvious that Hutchinson's strict adherence to the division of herbaceous versus woody plants has resulted in a less natural classification.

In the third edition of the same work, Hutchinson (1973) presented a new classification, in which an extended woody order Myrtales included Myrtaceae, Barringtoniaceae, Anisophylleaceae, Sonneratiaceae, Lythraceae, Rhizophoraceae, Lecythidaceae, Combretaceae, Punicaceae, Napoleonaceae, and Melastomata-

ceae. Crypteroniaceae and Oliniaceae were retained in Cunoniales and Penaeaceae in Thymelaeales. The herbaceous order Onagrales was there restricted to Onagraceae, Trapaceae, Haloragaceae (incl. *Hippuris* and *Gunnera*), and Callitrichaceae; whereas Dialypetalanthaceae were placed beside Rubiaceae in Rubiales, a very reasonable position in the light of some of its attributes.

Thorne (1968, 1976, 1981) by preference has wider ordinal and familial concepts. He restricts the superorder Myrtiflorae to the Myrtales, in which he now treats Lythraceae (incl. Punicoideae and Sonneratioideae), Penaeaceae, Oliniaceae, Trapaceae, Crypteroniaceae, Melastomataceae (incl. Memecyloideae), Combretaceae (incl. Strephonematoideae), Myrtaceae (incl. Psiloxyloideae), and Onagraceae. In the 1976 version of his classification he had included Thymelaeaceae in Myrtales, but in the latest treatment (Thorne, 1981) has returned Thymelaeaceae to Euphorbiales where he earlier (1968) had placed them. These families comprise what we shall treat as the 'core group' of families in Myrtales. Thorne has placed Rhizophoraceae and Haloragaceae in separate suborders of Cornales, and, in all versions of his classification has treated Lecythidaceae in Theales as the separate suborder Lecythidineae. He has included Dialypetalanthus among taxa incertae sedis, however, he now regards this genus as closely related to, or perhaps better included in, Rubiaceae of Gentianales.

Cronquist (1968) in his Myrtales included Sonneratiaceae, Lythraceae, Penaeaceae, Crypteroniaceae, Thymelaeaceae, Trapaceae, Dialypetalanthaceae, Myrtaceae (incl. Heteropyxis), Punicaceae, Onagraceae, Oliniaceae, Melastomataceae, and Combretaceae, giving the order approximately the same circumscription as that accepted by Thorne in 1976. Cronquist placed Lecythidaceae in the separate order Lecythidales, and Haloragaceae, Hippuridaceae, Gunneraceae, and Theligonaceae in an order named Haloragales. Further, Rhizophoraceae, as in Thorne's classification, were placed in Cornales, though Cronquist (1981) now prefers to treat Rhizophoraceae in their own order, Rhizophorales.

In his classification of 1981, Cronquist placed Dialypetalanthaceae in his Rosales, Theligonaceae in Rubiales, and Hippuridaceae in Callitrichales, leaving Haloragaceae and Gunneraceae in the order Haloragales.

Takhtajan (1959, 1966, 1969) included in the Myrtales Lythraceae, Sonneratiaceae, Punica-

ceae, Rhizophoraceae, Anisophylleaceae, Combretaceae, Lecythidaceae (sensu lato), Myrtaceae, Melastomataceae, Oliniaceae, Penaeaceae, Onagraceae, and Trapaceae. He placed Crypteroniaceae in Saxifragales near Brunelliaceae (cf. Cronquist, 1981). Takhtajan's Hippuridales (= Haloragales) included Haloragaceae, Gunneraceae, and Hippuridaceae and were placed next to Myrtales. Thymelaeales, with only Thymelaeaceae, were placed in sequence with Euphorbiales and were not considered by Takhtajan as related to Myrtales.

In a revised version of his angiosperm classification, Takhtajan (1980) widened the circumscription for his order Myrtales, which was divided into four suborders: Myrtineae, with the families of his order Myrtales from 1969 plus Crypteroniaceae; Haloragineae, with Haloragaceae (excl. Gunnera and Hippuris); Rhizophorineae, with Rhizophoraceae (incl. Anisophylleaceae, Legnotidaceae, and Polygonanthaceae); and Lecythidineae, with Lecythidaceae (incl. Asteranthaceae, Barringtoniaceae, Foetidiaceae, and Napoleonaceae). This new classification approaches closely that of Dahlgren (1980a); wherein, however, the Lecythidaceae are placed in Theales and the ordinal circumscription is slightly different.

Stebbins (1974) basically followed Cronquist (1968), but did include Rhizophoraceae in Myrtales. Like Cronquist, he treated Lecythidaceae in an order of their own.

Dahlgren, in his classification of 1975a, gave Myrtales the following circumscription: Lythraceae (incl. Sonneratiaceae), Punicaceae, Rhizophoraceae (incl. Anisophylleaceae), Crypteroniaceae, Combretaceae, Oliniaceae, Melastomataceae, Penaeaceae, Myrtaceae (incl. Heteropyxis), and Onagraceae, and in this order also included Dialypetalanthaceae, but remarked that the position of that family was uncertain. Trapaceae were excluded from the order as a consequence of the lack of endosperm formation and other details [but were reinstated in Myrtales in his later system (Dahlgren, 1980a; Dahlgren et al., 1981)]. Haloragaceae (excl. Hippuris and Gunnera) were treated in a separate order next to Myrtales, and Lecythidaceae with their segregates were placed in Theales. As in Takhtajan's classification, Thymelaeaceae were placed in Thymelaeales adjacent to Euphorbiales.

In the revised classification of 1980a, Dahlgren included in Myrtales the families Myrtaceae, Psiloxylaceae, Oliniaceae, Melastomataceae, Pen-

aeaceae, Crypteroniaceae, Lythraceae, Sonneratiaceae, Punicaceae, Combretaceae, Onagraceae, and Trapaceae. Haloragaceae and Rhizophoraceae were placed in separate orders next to Myrtales in the Myrtiflorae; whereas, Anisophylleaceae and Dialypetalanthaceae with some reservations were considered to be possibly cornalean.

Briggs and Johnson (1979) suggested a new classification of the former myrtalean families, distributing them in two orders, Myrtales sensu stricto and Lythrales, although these have widely different circumscriptions than have the corresponding orders in Hutchinson's system of 1959. Myrtales sensu stricto of Briggs and Johnson included Myrtaceae, Psiloxylaceae, Melastomataceae, Oliniaceae, and Penaeaceae; whereas, their Lythrales included Lythraceae, Sonneratiaceae, Punicaceae, Trapaceae, Combretaceae, Onagraceae, and Crypteroniaceae. [They have since (this symposium) dropped this division of the myrtalean families into two orders.] Haloragaceae, according to them, are possibly related to Myrtales and Lythrales, and Rhizophoraceae are suspected to be heterogeneous with possibly a thealean affinity. Thymelaeales, in accordance with various previous authors, are believed to be allied to Euphorbiales and Malvales. Lecythidaceae are also excluded, and Dialypetalanthaceae are regarded as gentianalean or rubialean (these orders are united in some systems). This classification will be discussed further in this paper.

Here, the order will be circumscribed largely as by Dahlgren (1980a), and by Thorne (1981), although the familial rank will be treated somewhat differently. One of us (Dahlgren) prefers smaller, homogenous families and recognizes as many as 14 families [Onagraceae, Trapaceae, Lythraceae (incl. Punicaceae and Sonneratiaceae). Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, Melastomataceae, Psiloxylaceae, Heteropyxidaceae, and Myrtaceae]. For convenience this treatment will be used throughout this survey. Thorne, on the other hand, includes Heteropyxidaceae and Psiloxylaceae in Myrtaceae and Memecylaceae in Melastomataceae. In all other respects, we are in agreement.

DEFINITION OF THE ORDER

Members are woody or herbaceous, terrestrial or rarely aquatic, ranging from huge trees to small annual herbs. The tap root is usually well developed.

Vascular strands are bicollateral in all the families and (as far as known) in nearly all species. Nodes are largely unilacunar (but trilacunar in Alzateaceae). Vessel elements have simple perforation plates (or very rarely scalariform perforation plates) and vestured pits (van Vliet, 1978). (Internal phloem and vestured pitting in this order are extremely important and define the order along with other distinctive features.) Wood rays vary between uni- and pluriseriate (even within most families), are mostly to 3 cells wide, and heterocellular to homocellular; ray cells often have gummy deposits; some of the axial parenchyma in scattered families generally consisting of vertical crystalliferous strands (Cronquist, 1981). Phloem of young twigs is often tangentially stratified into hard and soft layers. Sieve-tube plastids accumulate starch but never protein.

Leaves are typically opposite but quite often alternate, rarely verticillate, simple, either petiolate or sessile, rarely (in Onagraceae; Cronquist, 1981) lyrate-pinnatifid: The leaf margin is generally entire, but several genera of the Onagraceae and certain Lythraceae are provided with teeth ("Fuchsioid teeth") similar to those in Rosaceae, and Trapa has unique teeth having a double apex (Hickey, 1981, unpubl. data). Primary venation is pinnate, secondary venation most often brochidodromous, and tertiary venation obliquely and irregularly percurrent (Hickey & Wolfe, 1975). Stipules are present in nearly all families as rudimentary, either lateral or axillary, structures, the latter frequently dissected into several to numerous, small, finger-like projections (rarely long hairs). Ridges or wings of stems often end at the nodes in acute or acuminate tips, which should not be confused with stipules.

Branched sclereid idioblasts (foliar sclereids) are common in several families and tracheoids with spiral or annular wall thickenings are sometimes present. Schizolysigenous secretory cavities are present in the Psiloxylaceae and Myrtaceae. Hairs are sparse or lacking in some groups (e.g., Penaeaceae); when present, they are often unbranched, but especially in Melastomataceae are multicellular and complex, and in Combretaceae often form peltate or scale-like structures. Short, marginal hairs are present on the leaves in certain Onagraceae and Lythraceae. Stomata are anomocytic in most families but often anisocytic or polocytic in at least Onagraceae and Melastomataceae. Paracytic, procytic, and diacytic types also occur.

Inflorescences are variable but fundamentally

derivable from an anthotelic primary condition (see Briggs & Johnson, 1979). Suppression or amplification explain diverse inflorescences. Derived are, for example, the racemes (often associated with zygomorphic flowers).

Flowers are usually bisexual, generally adapted to insect or bird pollination, actinomorphic or weakly (to rarely strongly) zygomorphic, mostly 4- or 5-merous although sometimes 3-, 6-, or pleiomerous, perigynous to epigynous or sometimes semi-epigynous, without, or more often with, short to long hypanthium (an expanded, cup-shaped floral tube or receptacle) (Bunniger, 1972; Bunniger & Weberling, 1968), bearing mostly on its rim calyx-lobes, petals, and stamens, some of which may be reduced or absent (filaments are often more or less free from the hypanthium in Lythraceae and some Combretaceae, however). Calyx lobes are green or colored, sometimes conspicuously carnose, rarely shed as a cap at anthesis. Petals are usually present, then mutually free, unguiculate to basally cuneate, mostly red, violet, white, or yellow. Petals, when 5, are mostly with convolute aestivation, but when 4, with decussate aestivation.

The androecium is haplo- or diplostemonous (sometimes superficially obdiplostemonous), or secondarily polyandrous with centripetal or, more rarely, centrifugal developmental sequence, in the latter case often in a few clusters developed from the same number of primordia, associated with trunk-bundles. Reduction in stamen number within isomerous whorls is rare. Stamens have narrow to relatively broad, terete or flat filaments and basifixed or dorsifixed anthers, in some families with a conspicuously enlarged, compact and capitate (Penaeaceae) to variably elongated connective, without or with appendages (many Melastomataceae). Anther dehiscence is mostly by longitudinal slits or, in certain Myrtaceae and most Melastomataceae, by apical pores. The tapetum is glandular and generally binucleate.

Pollen grains are mostly free (tetrads are present in genera of Onagraceae, however), basically 3-colporate, but rarely colpate or porate. In several families they are provided with conspicuous pseudocolpi alternating with the true apertures; more rarely, viz. in some genera of Lythraceae, with twice as many pseudocolpi as true apertures. Viscin threads arise from the pollen grains in nearly all Onagraceae (exception: Circaea alpina L.); this family also is more variable in aperture condition than the other families. Pollen grains are usually 2-celled when dispersed (cf. Tobe &

Raven, 1984c).

An annular disc structure is often present around the style or ovary, inside the stamens (or hypanthium).

The pistil is syncarpous, consisting of two or more (frequently four or five) carpels and provided with one, two, or more locules, rarely with incomplete septa. The style (almost lacking in Psiloxylon) varies from apically branched (branches isomerous with carpels) to simple, with lobate to simple stigma, or with stigmatic areas rarely commissural and separate (as in some Penaeaceae; see below this family). The stigma is usually of the "dry" type (Heslop-Harrison & Shivanna, 1977), but at least in Melastomataceae and Onagraceae often of the "wet" type (Raven, pers. comm.). Placentation is mostly central and axile, or more rarely free-central (as in a few Lythraceae) or basal (as in most Penaeaceae) in the bi- to multilocular ovaries; parietal (as in a few Myrtaceae), or apical (as in all Combretaceae) in the unilocular ovaries.

Ovules are solitary to numerous per carpel, anatropous or rarely hemianatropous or campylotropous, crassinucellate, and generally bitegmic (unitegmic in some Myrtaceae). A primary parietal cell is cut off from the archesporial cell in all families studied (although this has not been verified satisfactorily for Myrtaceae). Embryo sac formation is mostly according to the Polygonum type, except in Penaeaceae (with the tetrasporic, 16-nucleate Penaea type), Onagraceae (with the monosporic, 4-nucleate Oenothera type), and Alzateaceae (with a bisporic, Allium type embryo sac; Tobe & Raven, 1984a). Endosperm formation is nuclear (but there is rapid endosperm nucleus degeneration in Trapaceae). The embryology of Myrtales has been reviewed by Tobe and Raven (1983a).

Fruits are most varied: capsules, berries, nuts, or samaras developed from superior or inferior ovaries.

The seed coat varies among the families of the order and tends either to have a fibrous exotegmen (i.e., outer layer of the inner integument) often combined with a sclerotic mesotesta (middle layer of the outer integument) or to lack a fibrous tegmen, then generally having a sclerotic mesotesta. Ripe seeds are generally without any or with a very thin layer of endosperm, this being used up during seed development. The embryo is variously differentiated, straight or more rarely curved or twisted, with anisocotyly in Trapaceae. The embryo stores fatty oils and aleuron in most families but does store starch in Trapaceae, and in some Myrtaceae and Melastomataceae.

Galli- and ellagitannins are normally present; flavonols (including methylated flavonols) are common, but flavones are rare or lacking. Proanthocyanins are present in some families. Triterpenes are common and triterpene saponins are present in at least some families. Various alkaloids are sporadically formed but are diverse and without great taxonomic significance. Cyanogenic compounds likewise are sporadically present in the order. Aluminum accumulation is conspicuous in at least three related families, and silica grains occur in certain Myrtaceae. Clustered or solitary crystals of calcium oxalate are commonly deposited in cells of the parenchymatous tissue; raphides are present in Onagraceae and rarely in Lythraceae. Iridoids, polyacetylenes, sesquiterpene lactones, glucosinolates, and benzylisoquinoline alkaloids are absent. Essential oils are present in secretory cavities in Myrtaceae.

Chromosome numbers tend to be multiples of 11 or especially $12 (X = 12 \text{ is considered a likely primary basic number by Raven, 1975), but show a considerable range of variation particularly in Onagraceae, Lythraceae, and Melastomataceae.$

This description is valid for the Myrtales if restricted to the "core families": Onagraceae, Trapaceae, Lythraceae, Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, Melastomataceae, Psiloxylaceae, Heteropyxidaceae, and Myrtaceae. With this circumscription the Myrtales seem to be homogeneous, natural, and easily definable. If the order were expanded, as recommended by some taxonomists, to include Thymelaeaceae, Lecythidaceae, Haloragaceae, or Rhizophoraceae, it would require considerable modification in each case. These families, considered by some as serious candidates for inclusion in Myrtales, will be discussed in more detail near the end of this paper.

A NOTE ON THE CIRCUMSCRIPTION OF THE FAMILIES OF MYRTALES

For the purpose of the following account on distribution of character states, the following notes may be adequate.

The Onagraceae present no problems and are circumscribed and subdivided as by Raven (1979), comprising 17 genera of ca. 675 species distributed among seven tribes.

Trapaceae consist of the genus Trapa only.

The family Lythraceae is more widely circumscribed here than in most contemporary literature. It includes Punicaceae, with the genus *Puni*-

ca (Levin, 1980, treats one of the species in the segregate genus *Socotria*), and Sonneratiaceae, with the probably rather distantly related genera *Sonneratia* and *Duabanga*.

The Combretaceae here include Strephone-mataceae (Venkateswarlu & Prakasa Rao, 1971), which consist of the single genus *Strephonema*. With the inclusion of the genus *Strephonema*, the Combretaceae (syn. Terminaliaceae) are circumscribed as in current works. The mangrove genera *Lumnitzera* and *Laguncularia* have probably adapted to their mangrove life by convergence.

Oliniaceae consist of the genus Olinia only.

Alzatea and Rhynchocalyx, which were treated in Crypteroniaceae by van Beusekom-Osinga and van Beusekom (1975), have here been excluded from this family and proved to be so distinct that they are each given family rank (Graham, 1984; Johnson & Briggs, 1984).

Penaeaceae (Dahlgren 1967a, 1967b, 1967c, 1968, 1971) consist of seven genera, Endonema, Glischrocolla, Saltera, Sonderothamnus, Brachysiphon, Stylapterus, and Penaea.

Crypteroniaceae, after the exclusion of Alzatea and Rhynchocalyx, consist only of Crypteronia, Axinandra, and Dactylocladus.

Memecyclaceae with some hesitation are here considered as distinct from Melastomataceae (by Dahlgren). It consists of six to eight genera, Mouriri, Lijndenia, Memecylon, Votomita, Spathandra, and Warneckea. Pternandra is also included, whereas the position of Astronia is doubtful.

Remaining are Psiloxylaceae (*Psiloxylon*), Heteropyxidaceae (*Heteropyxis*; Stern & Brizicky, 1958), and Myrtaceae, which are undoubtedly derivatives from the same ancestral stock. (Thorne considers *Heteropyxis* and *Psiloxylon* to represent subfamilies of Myrtaceae.)

DISTRIBUTION OF CERTAIN ATTRIBUTES IN THE FAMILIES OF MYRTALES AND SOME OTHER FAMILIES

The attributes discussed below and outlined as to their distribution in the myrtalean families and some allied families were selected on the basis of the following criteria:

- (1) they are either characteristic of the order or part of the order and frequently mentioned as "key" attributes;
- (2) most are reasonably well documented, although a few are not; and
- (3) they do not exhibit complicated patterns in the order.

Some of the attributes are often neglected to a great extent but deserve inclusion with the others. The selection is somewhat limited and cannot claim to include all the most essential items, but is thought to be representative in some degree, and to give an indication of:

- (1) distinctness of the order;
- (2) relationship among families of the order; and
- (3) degree of consistency of the attributes within families.

WOOD ANATOMY

As the wood anatomy is treated elsewhere in this symposium, by van Vliet and Baas, only a few remarks will be given here.

The core families of Myrtales are all characterized by the combination of bicollateral bundles (intraxylary phloem) (Fig. 1A) and vestured pits (Metcalfe & Chalk, 1950; van Vliet, 1978), a combination which is otherwise very rare in angiosperms and restricted to Thymelaeaceae (excl. Gonystyloideae), certain Euphorbiaceae, a few families of Gentianales, part of Vochysiaceae, and the genus *Centopodium* (= *Emex* proparte) of Polygonaceae (van Vliet & Baas, 1984). Thymelaeaceae and Loganiaceae, which appear to some as closely allied to Myrtales, will be discussed later. For different reasons each family is considered by us as not directly related to Myrtales.

From a purely wood-anatomical point of view it is obvious (van Vliet & Baas, 1984; Baas & Zweypfenning, 1979) that *Punica* as well as *Rhynchocalyx* (treated here as Rhynchocalycaceae) could well be included in Lythraceae, whereas *Sonneratia* and *Duabanga*, usually treated as the Sonneratiaceae, in different (and not always the same) wood-anatomical respects deviate somewhat more from Lythraceae. Thus the homogeneity of the former Sonneratiaceae must be reconsidered; *Sonneratia* and *Duabanga* diverge also in other respects (see p. 663). On the collected evidence they are both included in Lythraceae.

Further, Crypteroniaceae and Memecylaceae largely differ from Melastomataceae in having distinctly bordered pits and in lacking fiber dimorphism, and Memecylaceae also for the most part have solitary vessels and included phloem, which is not the case in Melastomataceae. This is taken to support treating Crypteroniaceae, Melastomataceae, and Memecylaceae as distinct families.

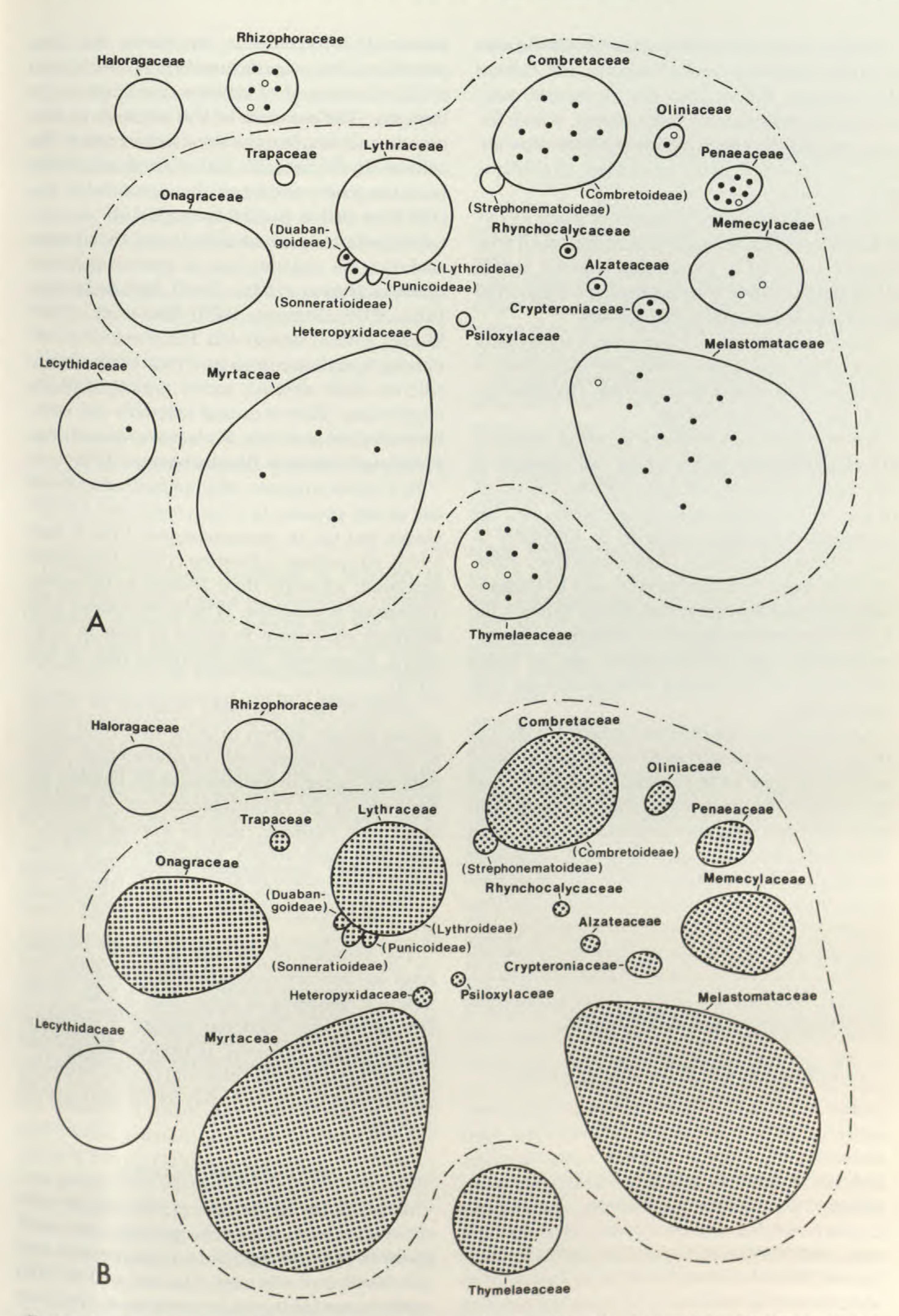


Figure 1. Distribution, in the myrtalean and some other families, of: −A. bicollateral vascular strands (dotting). −B. diffuse (●) and terminal (O) sclereids, according to Rao & Das (1979).

Strephonema differs from other Combretaceae in certain wood-anatomical respects, and Psilox-ylon similarly differs from the Myrtaceae, supporting the treatment of these genera, which for other reasons have been claimed to form separate units, as separate families or, at least, as subfamilies.

Alzatea also appears to be out of place in Lythraceae as well as in Crypteroniaceae, and it now appears it should be placed in a separate family (cf. Graham, 1984). This treatment is supported by various wood-anatomical details.

These indications, all based largely on the data of van Vliet and Baas (1984), are important in the general considerations of rank, circumscription, and interrelationships.

Some trends of evolution in wood anatomy are of significance in the order. An example is the reduction of pit borders and the limitation of pits to the radial walls in the fibers, i.e., the evolution from fiber-tracheids to libriform fibers. This has occurred in Lythraceae (incl. *Punica, Duabanga*, and *Sonneratia*), and in Onagraceae (there are also other similarities between the Lythraceae and Onagraceae), Oliniaceae, Melastomataceae, and Combretaceae, and in many Myrtaceae. In this respect these groups are thus specialized.

On the whole, the differences between the Lythraceae (sensu stricto) and Onagraceae in wood anatomy appear to be conspicuously few. There also seems to be great concordance in wood anatomy between Strephonematoideae and most Myrtaceae. Some of these similarities, as pointed out by van Vliet and Baas (1984), are, most likely, due to retention of primitive features and thus do not form a sound basis for phylogenetic conclusions, but others are similarities of specialization and therefore can be phylogenetically important, although convergent evolution in some of these features has surely occurred.

SCLEREID IDIOBLASTS OR FOLIAR SCLEREIDS

Rao and Das (1979) have surveyed the occurrence of foliar sclereids in angiosperms. Leaf sclereids (Fig. 1B) are common in the Myrtales, and are reported in Lythraceae (rare), Sonneratiaceae, Oliniaceae, Alzateaceae, Penaeaceae, Crypteroniaceae, Memecylaceae, Melastomataceae, and Myrtaceae (rare). In some Lythraceae and in Rhynchocalyx (Rhynchocalycaceae) they are unbranched and restricted to the leaf petioles; whereas, in Alzatea (Alzateaceae) they are

branched and present in the blades, this being possibly of some significance in the consideration of the distinctness of *Alzatea* in relation to Lythraceae. The presence of leaf sclereids in *Sonneratia* and *Duabanga* may also be noted in this context. In Penaeaceae, leaf sclereids are present in all the genera and have been described by Rao (1965) as well as by Dahlgren (1971).

Leaf sclereids are abundant and their shapes useful in the classification of species in Memecylaceae (Foster, 1946, 1947; Rao & Jacques-Félix, 1978; Bremer, 1979; Rao et al., 1980). Morley (1953) noted that the presence of terminal sclereids seems to be typical of this family, whereas their absence seems typical of Melastomataceae. Non-terminal sclereids do occur, however, in various Melastomataceae, e.g., Plethiandra (Rao & Bhattacharya, 1977).

In Crypteroniaceae, unbranched sclereids occur in leaf petioles in *Crypteronia* and *Dactylocladus*, but not in *Axinandra* (van Vliet & Baas, 1975). According to Keating (1982), Onagraceae lack foliar sclereids; their absence in the aquatic Trapaceae is expected. Within Myrtaceae, foliar sclereids are known to occur at least in *Angophora*, *Eucalyptus*, and *Syzygium* (Rao & Das, 1979).

Sclereids have not been recorded in Haloragaceae but are known to occur in several genera of Rhizophoraceae and Thymelaeaceae. Sclereids also occur in various taxa of Theales, perhaps not in the Lecythidaceae, but in Bonnetiaceae, for example, and in several genera of Theaceae sensu stricto. Furthermore, in Primulaceae, foliar sclereids are common, e.g., in *Dion*ysia (Bokhari & Wendelbo, 1976, where sclereids are classified).

The presence of sclereids and their variation must not be overemphasized as a taxonomic criterion. Considered at large (Rao & Das, 1979), they give a very scattered picture in the angiosperm system. However, in isolated famlies they may be conspicuously plentiful or may be absent, and in such cases they may be of phylogenetic interest.

SIEVE-ELEMENT PLASTIDS

As is shown by Behnke (1984), all Myrtales yet studied have sieve-tube plastids with starch grains (S-type plastids) but without protein crystalloids (P-type plastids). The fact that the Rhizophoraceae have protein crystalloids, which are numerous, rectangular or variously 4(or 5)-an-

gled, and of variable sizes (type PVc, sensu Behnke, 1981) may be taken as an indication that this family is not myrtalean. However, in dicotyledons a number of isolated families unexpectedly have P-type plastids of various shapes (Rhabdodendraceae, Cyrillaceae, Erythroxylaceae, Oxalidaceae, Connaraceae, Gunneraceae, Vitaceae, Buxaceae), a feature which may not, alone, be sufficient evidence for excluding them from orders with S-type plastids. Of the enumerated families, Erythroxylaceae are the family with the protein bodies most similar to those in Rhizophoraceae and Cyrillaceae, which should be considered in evaluating their phylogenetic relationships.

The fact that Myrtaceae, but not other Myrtales studied, contain crystalline protein in their sieve elements may indicate that they are somewhat isolated in the order.

PHYLLOTAXY

The most common condition in Myrtales is that the leaves are opposite. However, verticillate leaves occur in some genera, and the leaves are quite often disjunct-opposite or "scattered" ("alternate"), as in Psiloxylaceae, Heteropyxidaceae, many Myrtaceae, many Onagraceae (in the tribes Onagreae and Epilobieae), many Combretaceae (e.g., Terminalia and Buchenavia), and some Lythraceae. Whether in any of these families the leaves have truly spiral (disperse) phyllotaxy is not clear (see Johnson & Briggs, 1984).

To our knowledge all or nearly all taxa of Trapaceae, Oliniaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, and Melastomataceae (exceptions, e.g., Catantherea and Medinilla alternifolia Blume) have truly opposite or verticillate leaves, although they can be disjunct-opposite in fast-growing young shoots. The leaf rosettes of Trapaceae consist of decussate leaf pairs.

Thymelaeaceae, often placed in Myrtales, have disperse or opposite leaves. Among other families sometimes associated with Myrtales, Rhizophoraceae generally, but not consistently, have opposite leaves; Haloragaceae sensu stricto have three genera with exclusively disperse, three with either disperse or opposite, one (Haloragodendron) with only opposite, and one (Myriophyllum) with chiefly verticillate leaves (Orchard, 1975). Dialypetalanthaceae have opposite, decussate leaves. Finally, Lecythidaceae consistently have disperse leaves. Elaeagnaceae have

prevailingly disperse, but sometimes opposite, leaves.

STIPULAR STRUCTURES (by F. Weberling, Ulm)

In contradiction of the classical opinion, nearly all families belonging to the Myrtales are characterized by the occurrence of stipules (Weberling, 1955, 1956, 1958, 1960, 1963, 1966, 1968). They seem to be lacking usually in the Melastomataceae, and generally so in Memecylaceae, where they occur, however, in at least some taxa of *Mouriri* (Fig. 14B).

In most cases the stipules are diminutive ("rudimentary") and subulate (Fig. 2C), reaching only rarely a length of several millimeters. In most families of the Myrtales stipules represent a rather constant vegetative characteristic, as in Lythraceae (incl. Punicaceae and Sonneratiaceae), Trapaceae, Myrtaceae, Psiloxylaceae, Oliniaceae, Penaeaceae, and Crypteroniaceae (and also in the possibly allied families Rhizophoraceae and Haloragaceae), whereas in the other families they are present in some genera only. In Onagraceae, stipules are characteristic of five relatively primitive tribes, Jussiaeeae (Ludwigia), Hauyeae (Hauya), Fuchsieae (Fuchsia), Lopezieae (Lopezia), and Circaeeae (Circaea), but are absent in two advanced ones, viz., Epilobieae and Onagreae. In Combretaceae rudimentary stipules could be found only in species of Terminalia and in Buchenavia capitata Eichl.; perhaps they are present in Bucida buceras L. and Anogeissus leiocarpa Guill. & Perr. as well.

The ontogeny of the stipules in Myrtales displays usual features in their development. They appear at a very early stage of the leaf development, forming lateral excrescences from the leaf-base (Fig. 2A, D, F). Their further growth shows a more or less pronounced prolepsis. Sometimes they grow so rapidly that they temporarily have nearly the length of the entire leaf (Fig. 2B) or they may even exceed the leaf in length (Fig. 2D). They also attain their final proportions a long time before the leaf-blade does. Thus stipules which are more or less flattened are able to serve as bud-scales, whereas stipules which function as glands contribute to bud-protection by covering the buds with their mucous secretions.

Outside Myrtales as circumscribed here, stipules are present in Haloragaceae. In the pinnate leaves of Myriophyllum, more or less complete stipules at the very base of the leaf can be ob-

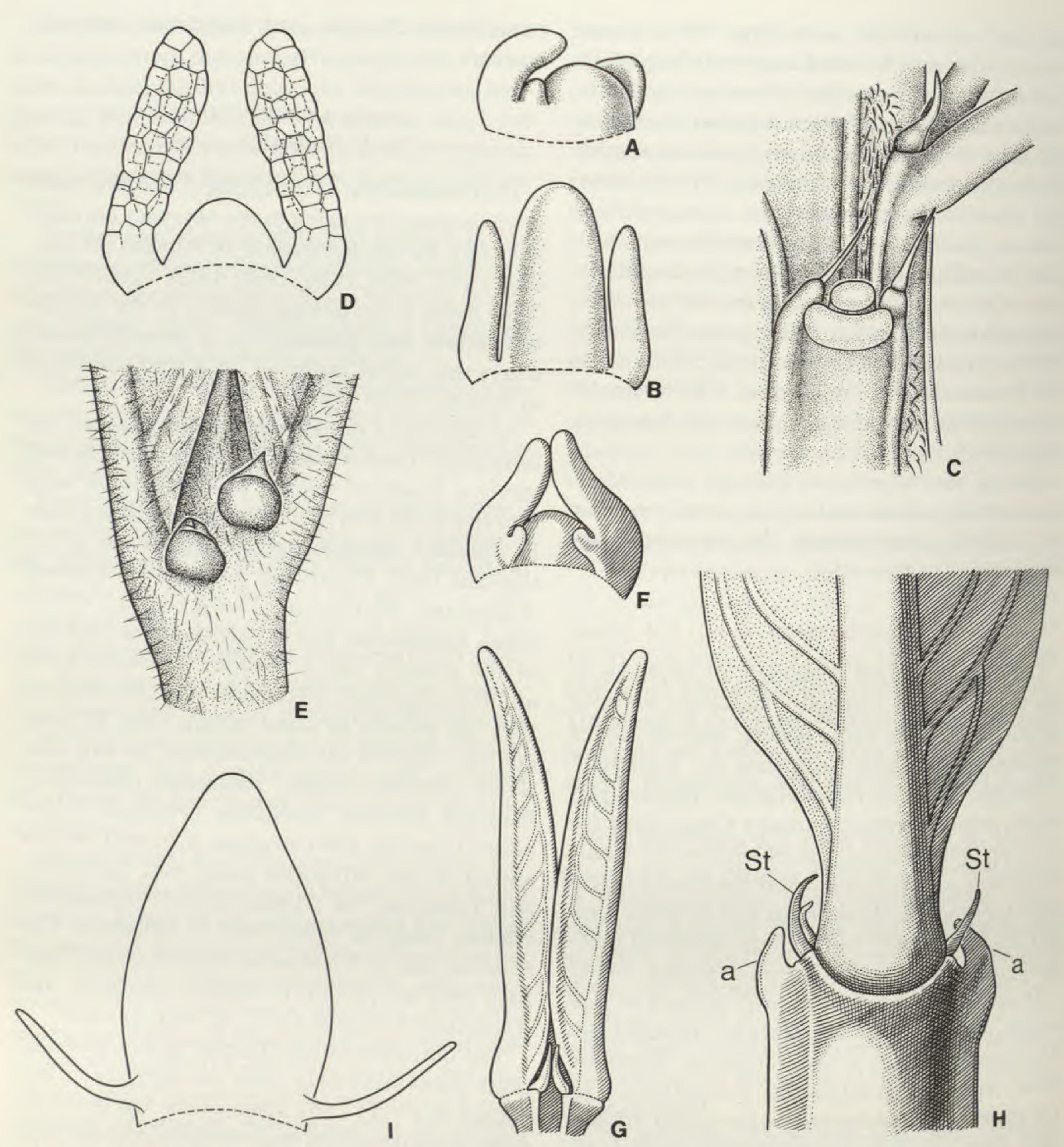


FIGURE 2. Stipules in the Myrtales. A-C. Lopezia racemosa Cav. (Onagraceae).—A. growing point with two leaf primordia, the larger one with primordia of stipules.—B. leaf primordium with stipules.—C. part of a stem bearing two leaf bases with stipules on the upper ends of ridges formed by the margins of decurrent leaves.—D. Circaea lutetiana L. (Onagraceae): leaf primordium with far developed stipules.—E. Ludwigia cf. uruguayensis (Camb.) Hara (Onagraceae): part of a stem with lower part of foliage leaves and stipules. F-I. Punica granatum L. (Punicaceae).—F-G. stages of leaf development.—H. base of young foliage leaf with decurrent wings ending in auricles (a) and rudimentary stipules (st)—I. cataphyll and stipules.

served. Above their insertion the formation of further leaflets still continues in a basipetal direction (Fig. 3G, H).

Commonly stipules are situated one on either side of the leaf axil. In this position they can be observed in *Lopezia* (Fig. 2C), *Ludwigia* (Fig. 2E), or in *Crypteronia* (Fig. 3C). In many taxa of Myrtales (e.g., many Myrtaceae and *Psiloxy*-

lon), however, they form two or more minute, subulate, or club-shaped processes shifted somewhat deeper into the leaf axil on either side of the leaf-base (Figs. 2H, 3A) or two groups of minute processes forming a transverse row across the base of the petiole (Fig. 3F). The latter type has been reported for most genera of Lythraceae by Koehne (1884, 1893, 1903), though within

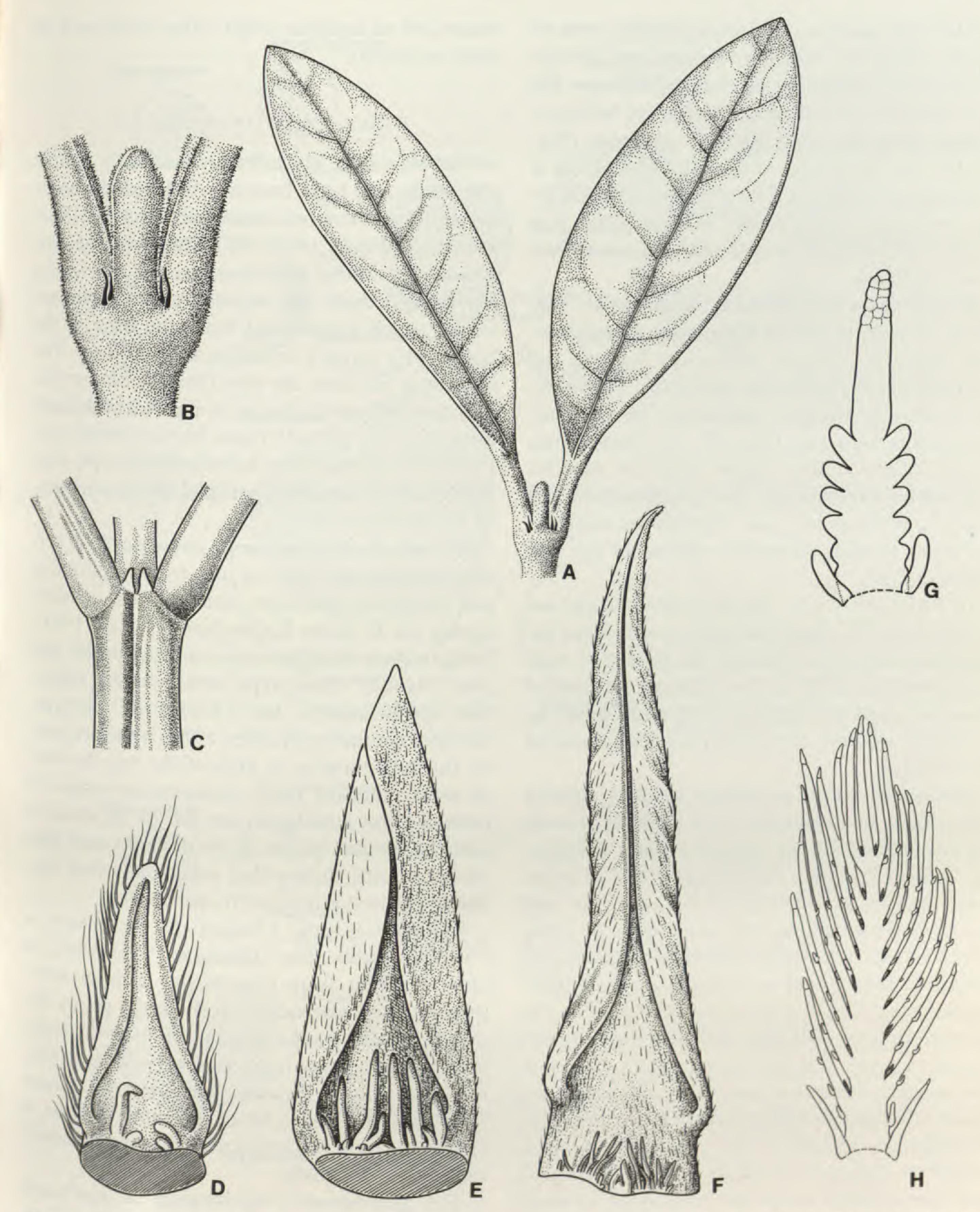


FIGURE 3. Stipules in myrtalean and some other families. A-B. Feijoa sellowiana Berg. (Myrtaceae).—A. opposite leaves with rudimentary stipules.—B. leaf bases in detail.—C. Crypteronia leptostachys Endl. (Crypteroniaceae); bases of oposite leaves with stipules.—D-F. Terminalia catappa L. (Combretaceae); different stages of leaf development (in D, 1.5 mm, in E, 3.5 mm, and in F, 10 mm long).—G-H. Myriophyllum pinnatum Britton (Haloragaceae); stages of leaf development, H representing a nearly fully developed leaf.

this family there are also taxa where leaves bear stipules in 'normal' position (e.g., Lagerstroemia and Lawsonia). Intrapetiolar rows of stipular processes also occur in Trapaceae, Penaeaceae,

many Myrtaceae, and some Combretaceae (and also in Lecythidaceae). Continuous morphological lines of intermediary forms (two- or three-lobed stipules a.o.) between stipules in 'normal'

number and position, and intrapetiolar rows of stipular processes indicate that the two groups of processes composing an intrapetiolar row are equivalents of two stipules. The same becomes evident from the study of their ontogeny (Fig. 3D–F). The dissection of the stipules may be a symptom of reduction. The displacement of stipular processes into the leaf axil probably is a result of an increased growth of the lower surface of the leaf-base.

In some Myrtales (Punica granatum L., Fig. 2F-H, Lafoënsia microphylla Pohl, Lagerstroemia indica L., Penaea mucronata L.) and the lecythidaceous Napoleona talbotii E. G. Baker, the stems are winged, apparently by the leafbases being decurrent (Fig. 2F, G). These wings are prolonged at their upper ends into auricles situated on either side of the leaf-insertion, like stipules, whereas the true stipules are subulate processes located somewhat deeper in the leafaxil (Fig. 2H).

In Rhizophoraceae, the Rhizophoroideae are characterized by large triangular to lanceolate interpetiolar stipules, whereas the genera of Anisophylleoideae differ by the alternate position of the leaves and the stipules being represented by a variable number of minute processes placed in the leaf axil.

Habitually, in the myrtalean families, stipules are present in connection with all leaves except the cotyledons. But in Angophora and Eucalyptus, genera in which the foliage leaves of all or most species are destitute of stipules, Carr and Carr (1966) found that the cotyledons of many species have rudimentary stipules. Johnson and Briggs (1984) report on stipules at the cotyledonary stage also in Arillastrum. The stipules can be two- or three-lobed or may be represented by several glandular processes situated on or near the margins of the leaf-base. The same is true for some other genera of Myrtaceae (Leptospermum, Callistemon, Melaleuca, etc.). Appendages which might be interpreted as rudimentary stipules have also been observed on the cotyledons in some species of Ludwigia (Dekker, pers. comm.). They are, however, missing on the cotyledons of other Onagraceae investigated, even those species in which the leaves are usually provided with stipules (Weberling, unpubl. data). Glandular minute stipules have been detected in the cotyledons of several Lythraceae, e.g., species of Cuphea and Lythrum (Weberling, unpubl. data).

In many Myrtales stipules also occur at the bases of the cataphylls (Fig. 2I) and at the bases of bracts. This fact indicates that cataphylls and

bracts are of laminar origin (also confirmed by their venation).

OTHER LEAF CHARACTERISTICS

The leaves in Myrtales are normally simple and entire and have basically brochidodromous to eucamptodromous venation (Hickey, 1981; Hickey & Wolfe, 1975). In certain lines of evolution, i.e., most Melastomataceae and many Myrtaceae, there are several main secondary veins, which branch out from the base of the blade, with tertiary veins being transverse. The difference between the two families Memecylaceae and Melastomataceae is significant (but not altogether sharp), both types being probably secondary to a typical brochidodromous type. Further trends of venation patterns are demonstrated by Hickey (1981).

As regards marginal teeth, these occur in certain Onagraceae, viz., in the tribes Epilobieae and Onagreae, and also, although less conspicuously so, in some Lythraceae (Hickey, 1981), being in these families conspicuously similar, and of a "Rosoid" basic type with a broad, craterlike apical hollow: the "Fuchsioid" subtype. Another similarity (Hickey, 1981) is the presence on the leaf margins in taxa of the two families of short marginal hairs. Independent origin of both of these structures, the former of which is quite particular, seems to be unlikely, and thus we agree with Hickey that most likely they represent original attributes in the order.

In the Trapaceae (*Trapa*) the teeth have a "unique double apex" (Hickey, 1981), which is quite different from that in the families mentioned. Teeth also occur rarely in the genus *Sonerila*, Melastomataceae (e.g., in *Sonerila tenuifolia* Blume), where they may vary considerably in length (Carlo Hansen, pers. comm.). These teeth do not seem to be of the same kind as in Onagraceae or Lythraceae; their filiform apex may represent a trichome.

The phylogenetic significance of leaf-tooth types is discussed by Hickey and Wolfe (1975), who state that they often show great homogeneity in families, orders, and larger groups and that conclusions can be drawn from their distribution. The Rosoid teeth in some Myrtales, if they are a residual attribute, indicate a possible connection with the Rosales and other orders possessing such teeth, such as Rhamnales, Rutales, Sapindales, Cunoniales, Vitales, and Cornales.

The leaf teeth in Lecythidaceae are of the "Theoid" kind (Hickey & Wolfe, 1975) and so

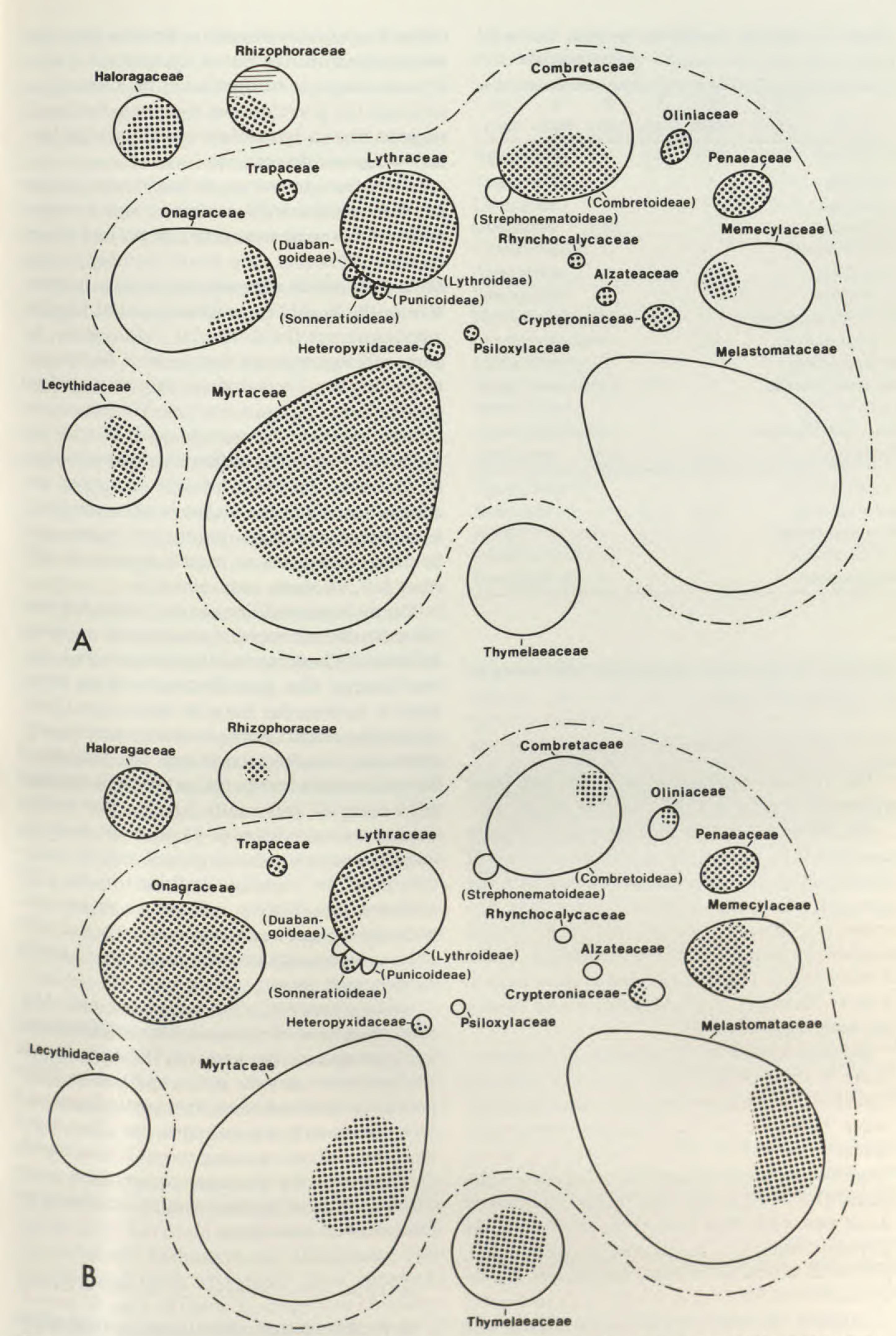


FIGURE 4. Distribution, in the myrtalean and some other families, of: -A. stipules, minute (dotting) or fairly large (hatching). -B. tetramery of perianth (dotting).

TABLE 1. Merous conditions in sepal and petal whorls in Myrtales and possibly related families.

	2- mery	3- mery	4- mery	5- mery	>5- mery
Onagraceae	(+)	(+)	+	(+)	(+)
Trapaceae	_	_	+	_	_
Lythraceae	_	-	+	(+)	+
Oliniaceae	_	-	(+)	+	-
Combretaceae	-	-	+	+	(+)
Alzateaceae	-	-	_	+	_
Penaeaceae	_	_	+	_	=
Rhynchocalycaceae	-	-	-	-	+
Crypteroniaceae		-	+	+	-
Memecylaceae	-	-	+	+	-
Melastomataceae	-	(+)	(+)	+	(+)
Psiloxylaceae	-	_	-	+	(+)
Heteropyxidaceae	-	-	_	+	_
Myrtaceae	-	-	(+)	+	(+)
Thymelaeaceae	-	-	+	+	(+)
Haloragaceae	(+)	(+)	+	_	-
Rhizophoraceae	-	(+)	+	+	(+)
Lecythidaceae	-	_	(+)	+	(+)
Elaeagnaceae	_	_	+	_	_

probably do not show connection with those in any myrtalean group.

MEROUS CONDITIONS OF PERIANTH

The merous conditions in sepal and petal whorls are shown in Table 1 and in Figure 4B.

The general trend in angiosperms is usually considered to be that an indefinite number of spirally set tepals, stamens, and carpels form the most primitive state; whereas 3-mery (as in Annonaceae, Aristolochiaceae, etc.) and 5-mery (numerous groups) evolve as secondary states, 4-mery mostly being considered as secondary to 5-mery. However, in the Myrtales 4- and 5-mery are both very common.

Merous conditions in perianth and androecium of the Myrtales have been discussed by Eyde (1977) in connection with the genus Ludwigia. This genus, unlike the other, almost consistently 4-merous Onagraceae, has a 5- or 6-merous perianth in a number of species. Eyde stated (1977: 653) that the "higher number of floral parts can occur in association with certain advanced features. For instance, in sect. Occarpon, with 5-merous flowers, and in sect. Oligospermum, where 5-mery is the rule and 6-mery occasional, the higher numbers are linked with 1-seriate ovules and a specialized endocarp." Be-

cause Ludwigia represents a phyletic line separated early from the rest of Onagraceae, 5-mery or more may not be derived in the Onagraceae, although the prevalence of 4-mery in this family suggests that its immediate ancestors might have had 4-merous flowers.

Lythraceae are more or less evenly divided between genera with 4-merous and 6-merous flowers with respect to sepal, petal, and stamen number. However, the locule number is most often 2-4, which suggests that 4-mery is primitive in the family (provided ancestral Myrtales had isomerous floral whorls). Additionally, zygomorphic genera are 6-merous, a further evidence that 6-mery is derived. Not all specialized genera, however, are 6-merous. The aquatic and marsh annuals, Ammannia and Didiplis, are 4-merous. Pentamerous flowers are common only in Decodon. There is variation in merous conditions among populations within species in some genera, but the 4-merous or 6-merous state is clearly dominant in most instances (A. Graham & S. Graham, pers. comm.).

The merous conditions in myrtalean and some other families, somewhat generalized, are shown in Table 1. The commonest conditions are 4-mery and 5-mery. The great frequency of the former state is noteworthy since in most other dicotyledonous orders 5-mery is much more frequent. However, merous conditions are variable in Myrtales, and it is even rather typical in the larger (and some of the small) families that merous conditions vary from (2-)3 to 6 or more. An outgroup comparison combined with an appreciation of the merous conditions in the order indicates that 5-mery is likely to be ancestral, although 4-mery has arisen very early and probably, subsequently become dominant in several evolutionary lines.

Among families often associated with Myrtales, 4-mery is common in Thymelaeaceae and Rhizophoraceae, dominant in Haloragaceae and Elaeagnaceae, and the only condition in Dialypetalanthaceae; whereas, in Lecythidaceae it is rare. Tetramery in floral parts has often been a consideration in regarding most of these families as related to the Myrtales or members of the order in spite of the fact that it is probably not the ancestral state here.

INFERIOR, SEMI-INFERIOR, OR SUPERIOR OVARY

In the Myrtales the floral tube is either adnate to all or part of the ovary walls (epigynous and

hemi-epigynous states respectively) or surrounds the ovary either tightly or loosely (perigynous states). The distribution of these states is shown in Table 2 and Figure 5A.

Because hypogyny and perigyny are considered to precede hemi-epigyny and epigyny and because several families are heterogeneous in this respect, it is obvious that adnation between floral tube and ovary has occurred in several evolutionary lines.

The floral tube (or hypanthium) is quite varied in length and may be short or long, and loose or tight around the ovary. Where it can be called a hypanthium, it bears on its edge sepals, petals, and frequently also one or two whorls of stamens or numerous stamens, although stamens can also be borne on the inner side of the hypanthium, or near its base.

In perigynous flowers of most Lythraceae, all the filaments are nearly or wholly free from the hypanthium. This condition may be considered either as an original state or as a separate, derived condition in relation to that where the filaments are inserted on the hypanthium edge. Exceptions are found in Lawsonia, where the stamens are inserted on the inner side of the hypanthium, and in Sonneratia, Duabanga, and some species of Cuphea, where they are inserted on or near its rim. The first two genera, often referred to Sonneratiaceae, thus deviate from most other Lythraceae in having the stamens inserted on the rim of the hypanthium. Also Rhynchocalyx (Rhynchocalycaceae), which is sometimes referred to Lythraceae, has the stamens inserted on the rim of the hypanthium.

In epigynous flowers of Myrtales a hypanthium continuing beyond the ovary is sometimes missing, as in *Ludwigia* (Onagraceae).

Within Myrtales the perigynous flower, found in most Lythraceae, and in all Penaeaceae, Rhynchocalycaceae, Alzateaceae, Psiloxylaceae, Heteropyxidaceae, Trapaceae, and in a great part of Melastomataceae but in very few Myrtaceae, is undoubtedly the ancestral condition. In Melastomataceae, there is a range of variation from perigyny to epigyny, and in Combretaceae the flowers are hemi-epigynous (Strephonema) or epigynous, and the immediate ancestors of each family must have had perigynous to hemi-epigynous flowers. Memecylaceae, Oliniaceae, Onagraceae, and most Myrtaceae have epigynous flowers. In each of them the epigynous condition apparently evolved early, but the ancestors of each family presumably had perigynous flowers,

TABLE 2. Gynous conditions in Myrtales and possibly related families.

	Hypo/ perigyny	Hemi- epigyny	Epigyny	
Onagraceae		_	+	
Trapaceae	+	(+)	-	
Lythraceae	+	(+)	(+)	
Oliniaceae		_	+	
Combretaceae	-	-	+	
Alzateaceae	+	-		
Penaeaceae	+	_	-	
Rhynchocalycaceae	+	-	-	
Crypteroniaceae	(+)	+	-	
Memecylaceae	-		+	
Melastomataceae	+	+	+	
Psiloxylaceae	+	-	_	
Heteropyxidaceae	+	-	-	
Myrtaceae	(+)	+	+	
Thymelaeaceae	+	-	_	
Haloragaceae		_	+	
Rhizophoraceae	(+)	(+)	+	
Lecythidaceae	-		+	
Elaeagnaceae	+		-	

because other families to which they are closely related have representatives with perigynous flowers. Lythraceae, in which perigynous flowers are combined in various members with a number of other probable ancestral states, therefore take a central position in the order.

Among the families often associated with Myrtales, Elaeagnaceae and Thymelaeaceae have perigynous flowers. Rhizophoraceae exhibit a range of variation from perigynous to epigynous flowers, while Dialypetalanthaceae, Haloragaceae, and Lecythidaceae have epigynous flowers.

ONTOGENY OF FLORAL PARTS IN SOME MYRTALES

In a study of the ontogeny of the flower in representatives of Lythraceae (incl. *Punica*), Onagraceae, and Myrtaceae, Mayr (1969) found the following features:

The histogenesis of the organs of the flower shows different participation of cell layers, the relative number of cells in the basal level of the primordia being the critical factor.

In Myrtaceae the sepals and petals are more or less simultaneous in ontogeny but in Lythraceae (also in *Punica*) and Onagraceae the petals develop considerably later than the sepals.

The "epicalyx" found in many Lythraceae (see

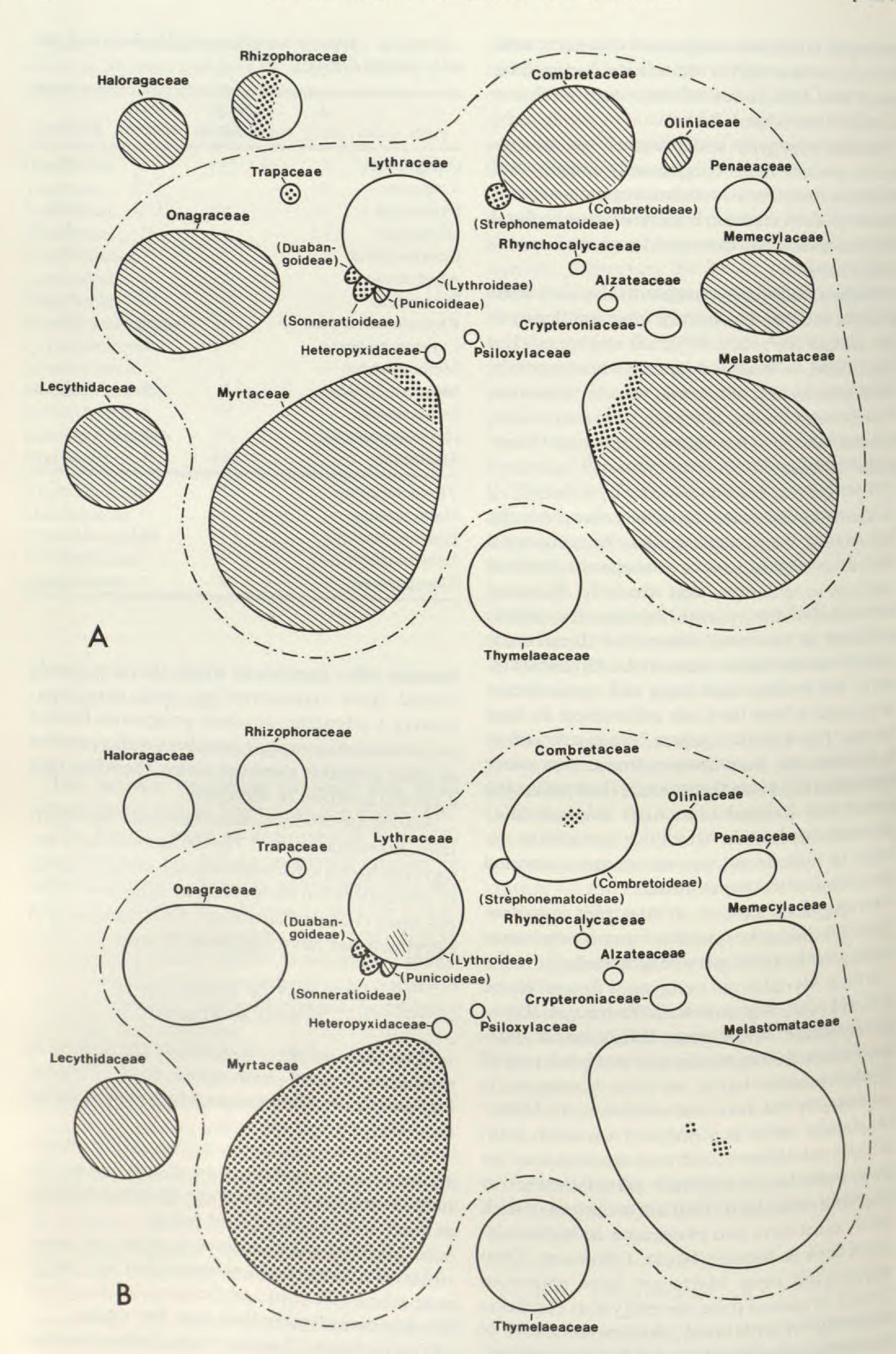


Fig. 8G) is interpreted as processes from the congenitally fused sepals (comparable to commissural stigmas). The position of Coridaceae, which is similar in this respect, is discussed on p. 686.

In androecia with numerous, bundled stamens, the organogeny of the stamens within the bundles is centripetal in Myrtaceae but centrifugal in Lagerstroemia and Punica of the Lythraceae.

The androecium of all taxa with two whorls of stamens is actually diplostemonous. Where it appears obdiplostemonous (as in Onagraceae), this condition depends on primary differences in size and secondary displacement in the course of growth.

Some Onagraceae have commissural stigmas (which is also the case in *Penaea* and *Stylapterus* of the Penaeaceae; see under this family below, and Dahlgren, 1967a, 1968).

Mayr (1969) concluded that, among the families investigated, Myrtaceae stand apart from the other three in several important details.

MERY AND DEVELOPMENTAL SUCCESSION IN ANDROECIA

In the Myrtales, diplostemony is no doubt basic.

Haplostemony occurs in Trapaceae, Oliniaceae, Alzateaceae, Penaeaceae, and Rhynchocalycaceae, and in disparate genera of Lythraceae and Melastomataceae, a few genera of Combretaceae and Onagraceae, two genera (Crypteronia and Dactylocladus) of three in Crypteroniaceae, and (as a case of reduction in a polystemonous whorl) in at least Myrrhinium of Myrtaceae. In Combretaceae, the flowers in Meiostemon and Thiloa as well as in one species of Terminalia are regularly haplostemonous, one species of Thiloa having staminodia representing the second whorl; in Conocarpus the androecium is sometimes reduced from ten stamens to varying numbers down to five by abortion (Stace, pers. comm.). In Onagraceae, Circaea, Lopezia, some species of Clarkia and Ludwigia, and one species of Camissonia have haplostemonous flowers (Eyde, 1977), all these cases being no doubt secondary in relation to diplostemony. In Melastomataceae, haplostemonous androecia are in the minority but are scattered in a number of genera.

It is also fairly obvious that in Lythraceae there have been both reduction and multiplication of stamen number from a diplostemonous condition. Reduction has occurred either as loss of episepalous stamens (Orias, Lawsonia, Capuronia), or episepalous stamens (Tetrataxis, Diplusodon, Galpinia, Pleurophora). Multiplication has occurred by increase in the epipetalous whorl (Ginoria, Lagerstroemia) or increase in the episepalous stamens (Diplusodon). Although the evolutionary relationships among the genera are not clear, it does appear that the loss or gain of staminal whorls has occurred independently more than once in Lythraceae and both loss and gain can occur within a single genus. An interesting staminal feature in Lythraceae is that stamens are often of two distinct lengths, with the episepalous ones always longest. (All this according to A. Graham & S. Graham, pers. comm.)

The occurrence of numerous stamens in certain Myrtales, as in other orders, such as Malvales, Theales, Caryophyllales (Chenopodiales), and Loasales, is no doubt a derived condition that has evolved from a diplo- or haplostemonous state (Leins, 1964), providing greater pollen production, especially in large flowers. This does not mean that the original ancestors of the angiosperms could not have had an indefinite number of stamens, which most likely were spirally arranged.

Much emphasis has been laid on the developmental sequence (initials or anthesis, according to authors) of stamens in polyandrous taxa, i.e., whether the groups of stamens develop centrifugally or centripetally. Leins (1964) distinguished three groups for their subdivision, but there must be many more than three evolutionary lines for polymerous androecia. Cronquist (1968) and Takhtajan (1969) have laid much stress on whether orders have centripetal or centrifugal androecial development, and Merxmüller and Leins (1971) have further elucidated the occurrence and taxonomic significance of these types. Multistaminal androecia have surely evolved secondarily in independent lines, examples being the Capparales (Capparaceae), Car-

FIGURE 5. Distribution, in the myrtalean and some other families, of: —A. perigynous (blank), hemi-epigynous (dotting), and epigynous (hatching) flowers.—B. multistaminate androecia with centrifugal (hatching) and centripetal (dotting) developmental succession.

yophyllales (Aizoaceae, Cactaceae), Loasales (Loasaceae), Theales (several families), Thymelaeales (Thymelaeaceae: Gonystylus), Malvales (several families, e.g., Tiliaceae, Sterculiaceae, Malvaceae), Violales (independently from the preceding?: various Flacourtiaceae, Begoniaceae, etc.), perhaps also (?) Rosales (Chrysobalanaceae: Couepia), and Myrtales. In Rosales, the stamens are generally arranged in several whorls which tend to have stamens in a multiple number of that in the perianth whorls, and Chrysobalanaceae may not belong here. Also in palms, the stamens, no doubt, have increased secondarily in number, with different developmental sequences as a result (Uhl & Moore, 1980). A similar condition occurs in Velloziaceae; and in Alismataceae a secondarily multistaminal condition develops from initials superposed on the primary fewer ones, resulting in numerous whorls of stamens (Sattler & Singh, 1978, and other papers).

It seems that what is taxonomically important is not the developmental direction in itself but rather along which evolutionary lines these androecia evolved, i.e., whether the multistaminal condition in various Myrtales has evolved along the same lines or not. Within Myrtales there are families with multistaminal as well as diplo- and haplostemonous androecia, e.g., Lythraceae, Myrtaceae, Melastomataceae, and Combretaceae. There seems thus to be a general tendency, within the order, for reduction as well as multiplication of stamens.

There is some regularity in the distribution of these secondarily multistaminal androecia and their initiation. Those of Myrtales are generally known to be centripetal, but Mayr (1969, see above) observed that *Punica* and *Lagerstroemia* (Lythraceae) have centrifugal development, as in most Lecythidaceae and various other Theales (see Fig. 5B).

Within Melastomataceae, the genus Astrocalyx may have up to ca. 65 stamens per flower, and in *Plethiandra* the stamens may be 20–30 in number. The developmental sequence of the stamens in these genera has apparently not been studied.

Diplostemony seems to be basic in Myrtales and wide-spread in the order, occurring in several of the larger families: Lythraceae, Combretaceae, Melastomataceae, and Onagraceae.

POLLEN FEATURES, PARTICULARLY OCCURRENCE OF PSEUDOCOLPI

Pollen morphology of Myrtales and possible allied groups is described separately in this sym-

posium by Patel et al. (1984); hence we restrict ourselves to some general comments. The pollen grains in the core families of this order seem to be basically 3-colporate, although two to more than five apertures have been reported. Further the pollen grains are basically tectate and frequently characterized by pseudocolpi (intercolpate furrows or "rugae," sensu Erdtman, 1952). The pseudocolpi are not actual apertures but conspicuously colpus-like thin parts of the exine. In their early ontogeny they differ from true apertures by not being subtended by a thick layer of intine (Thanikaimoni, pers. comm.). Pollen tetrads occur in some groups, especially in Onagraceae, where another peculiarity, the occurrence of viscin threads, is a characteristic feature.

Pseudocolpi (Fig. 6) are recorded in the families Lythraceae, Oliniaceae, Combretaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, and Melastomataceae (incl. Memecyloideae) but are absent (or very indistinct) in many Lythraceae (see below, incl. the Punicoideae, Sonneratioideae, and Duabangoideae), Trapaceae, Alzateaceae, Psiloxylaceae, Heteropyxidaceae, Myrtaceae, and Onagraceae. More or less distinct intercolpate depressions in the pollen grains connect the distinctly heterocolpate pollen grains with other types and make the feature somewhat vaguely defined. However, presence of pseudocolpi is so significant in Myrtales, and so rare outside the order, that we attach great phylogenetic significance to its distribution. The significance of pseudocolpi in the Crypteroniaceae (as circumscribed by van Beusekom-Osinga & van Beusekom, 1975), i.e., in the genera Crypteronia, Dactylocladus, Axinandra, Alzatea, and Rhynchocalyx, was elucidated, for example by Muller (1975). He found Alzatea to differ from the others in lacking pseudocolpi, thus contributing toward recognition of the heterogeneity of the family in that circumscription.

The relatively homogeneous family Lythraceae, however, shows great variation in the occurrence of pseudocolpi (see also Patel et al., 1984). Thus according to Erdtman (1952), Campos (1964), and S. Graham (pers. comm.), Lythraceae generally possess 3-colporate pollen grains (in Lafoënsia oracolpoidate, Campos, 1964). Nine genera have pseudocolpi, according to S. Graham (pers. comm.). In Lythrum, at least there are three pseudocolpi alternating with the three apertures, but in Ammannia, Crenea, Ginoria, and Nesaea there are six pseudocolpi, two pseudocolpi being present between two successive apertures. Fifteen other genera (according to

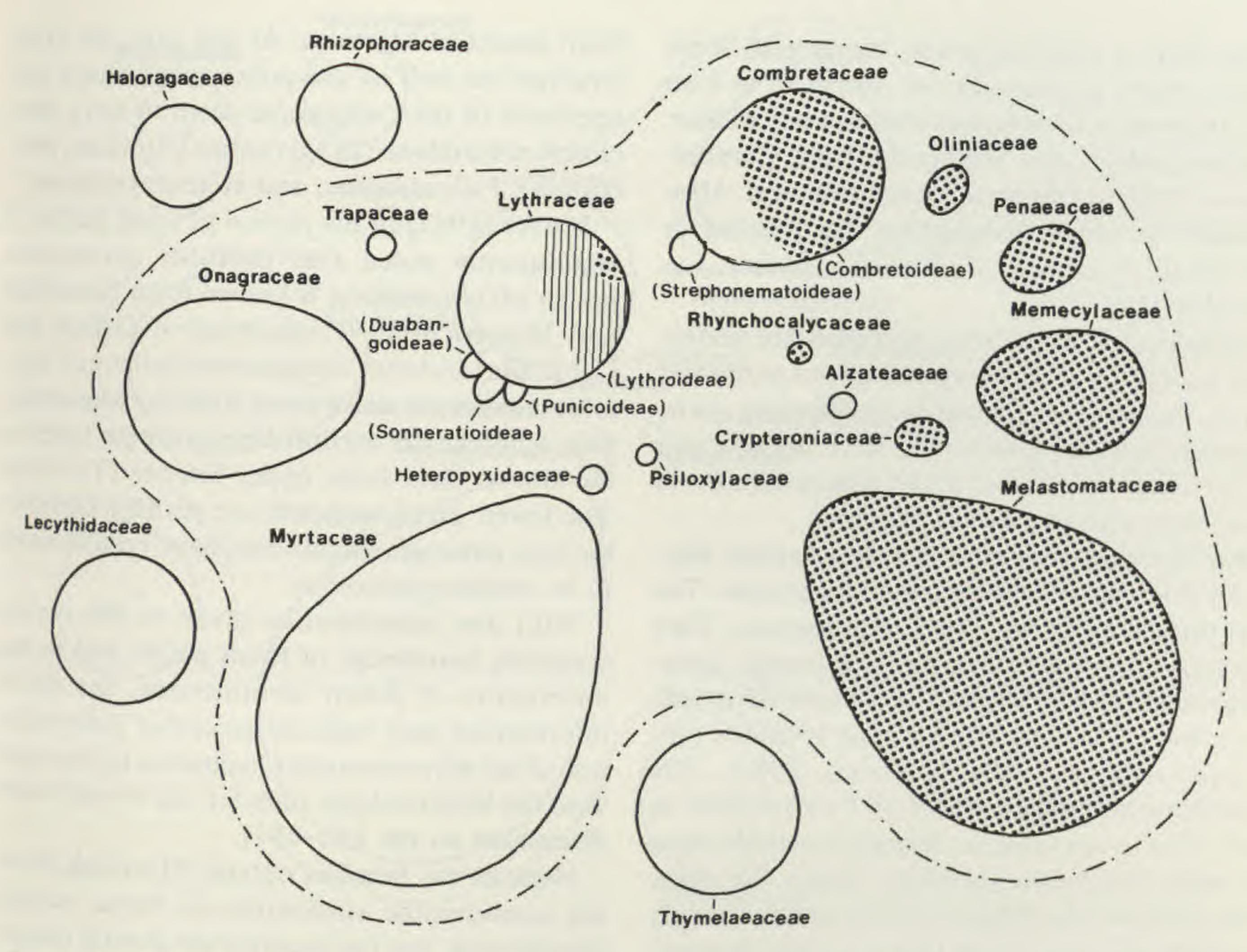


FIGURE 6. Distribution, in the myrtalean and some other families, of pollen grains without (blank) pseudocolpi, with pseudocolpi isomerous with apertures (dotting) and with pseudocolpi double the number of apertures (hatching).

S. Graham, pers. comm.), such as Adenaria, Cuphea, Diplusodon, Galpinia, Lafoënsia, Lagerstroemia, Pemphis, Pelurophora, Physocalymma, and Woodfordia, lack pseudocolpi. Rotala (Campos, 1964) may have incipient (or rudimentary!) pseudocolpi: "R. ramosior marquerait le passage entre les pollen tricolporés et héterocolpés" (Campos, 1964: 306). Here, as well as in the pollen grains of Lafoënsia, where the pseudocolpi are very faint, these could be interpreted either as incipient or reduced. A study of the lythraceous pollen morphology may indicate that (distinct or faint) pseudocolpi seem to occur in derived genera (A. Graham & S. Graham, pers. comm.), although this is not clear. In variation of occurrence and number of pseudocolpi (relative to apertures), Lythraceae are outstanding in the order, and it may be argued whether absence of pseudocolpi represents an original or (by secondary loss) an advanced state.

Sonneratia and Duabanga have angulo-aperturate pollen grains with short colpi (Muller, 1969, 1978). Distinct pseudocolpi are lacking, but in Sonneratia intercolpate depressions resembling

pseudocolpi may occur. According to Erdtman (1952) the pollen grains resemble those in *Diplusodon* of the Lythraceae, and Muller (1981) reports a pollen type, *Florschuetzia trilobata*, from the Oligocene and Miocene of Borneo, that combines lythraceous and sonneratiaceous characteristics. Also the pollen grains in *Punica* resemble those in other Lythraceae. They are 3- (or rarely 4-) colporate and likewise lack pseudocolpi.

Whether the very characteristic pollen grains in Trapaceae, with three meridional crests of folded exinous material meeting at the poles, represent a heterocolpate type or rather a type with pronounced intercolpate depressions, needs to be verified.

The heterocolpate pollen grain types thus do not represent a distinct category. They include very peculiar shapes, such as that in Oliniaceae, where the pseudocolpi are restricted to one hemisphere (Patel et al., 1984).

Nevertheless, there is evidence from this attribute, as from others, that the families or subfamilies with clearly heterocolpate pollen grains form a coherent group, along with some others, where pseudocolpi are absent or at least very indistinct (Lythraceae subfam. Punicoideae, Duabangoideae, and Sonneratioideae, Combretaceae subfam. Strephonematoideae and Alzateaceae) or where pseudocolpi are missing or "doubled" in number (Lythraceae subfam. Lythroideae).

Pseudocolpi, aside from Myrtales, are known only in Ehretioideae (Boraginaceae pro parte) and a few Fabaceae (Leguminosae) (Skvarla, pers. comm.), and the tendency to have pseudocolpi is not likely to have evolved independently in more than one line within Myrtales.

Pseudocolpi are absent in Psiloxylaceae, Heteropyxidaceae, Myrtaceae, and Onagraceae. The first three families are fairly homogenous. They have (2–)3(–4) apertures and are mostly triangular, angulaperturate, very often syncolp(or)ate, with thin exine, and with a psilate to faintly patterned, scabrate surface (Schmid, 1980). The syncolp(or)ate pollen grains of *Psiloxylaceae* as well as *Heteropyxidaceae* strongly resemble those in many Myrtaceae (Schmid, 1980). We agree with Johnson and Briggs (1984) that this strongly supports the assumption that syncolp(or)ate pollen grains occurred in the common ancestor of these three families.

The Onagraceae are palynologically very distinct in the order. The pollen grains are noteworthy by the often triangular shape with three or more protruding, "papillose" apertures, the mechanism of tetrad cohesion (Skvarla et al., 1975), and the fine structure of the exine, in particular the ektexine, which is granular, "beaded," delicately branched, etc. (Skvarla et al., 1976), and especially by the constant presence of viscin threads (Skvarla et al., 1978), matched only in two other angiosperm families, viz., Ericaceae and Fabaceae. The relative number per pollen grain and the surface structure of these threads are variable in Onagraceae and supply some characters of interest for the division of the family. It can be claimed that the character-states associated with the pollen grains in Onagraceae along with many other distinctive features indicate that the family was differentiated early

from ancestral Myrtales. At any rate, the exine structure as well as the pollen grain shape and apertures of the Onagraceae seem to have their closest resemblance in Myrtaceae (Nowicke, pers. comm.), Psiloxylaceae, and Heteropyxidaceae.

Muller (1981) in his review of fossil pollen of angiosperms noted that probably myrtaceous pollen (Myrtaceidites) is known from Santonian and Maestrichtian (Cretaceous) of Gabon and Colombia, and that onagraceous pollen (cf. Epilobium type) are also known from the Maestrichtian, whereas the earliest heterocolpate types so far known date from upper Eocene (Tertiary). The latter, Heterocolpites, are perhaps combretaceous, although similar ones have been claimed to be melastomataceous.

With due consideration given to the yet incomplete knowledge of fossil pollen and to the uncertainty of pollen identification, the above information may indicate an earlier differentiation of the Myrtaceae and Onagraceae pollen types than the heterocolpate ones (cf. the evolutionary discussion on pp. 680–681).

None of the families outside Myrtales, showing considerable similarities to them, possess pseudocolpi, but the tricolporate general pattern in Rhizophoraceae is of the basic type found in the Myrtales (Lythraceae pro parte, Alzateaceae), whereas the pollen grains in Lecythidaceae vary from colpate to colporate (via "colporoidate" transitions, Erdtman, 1952).

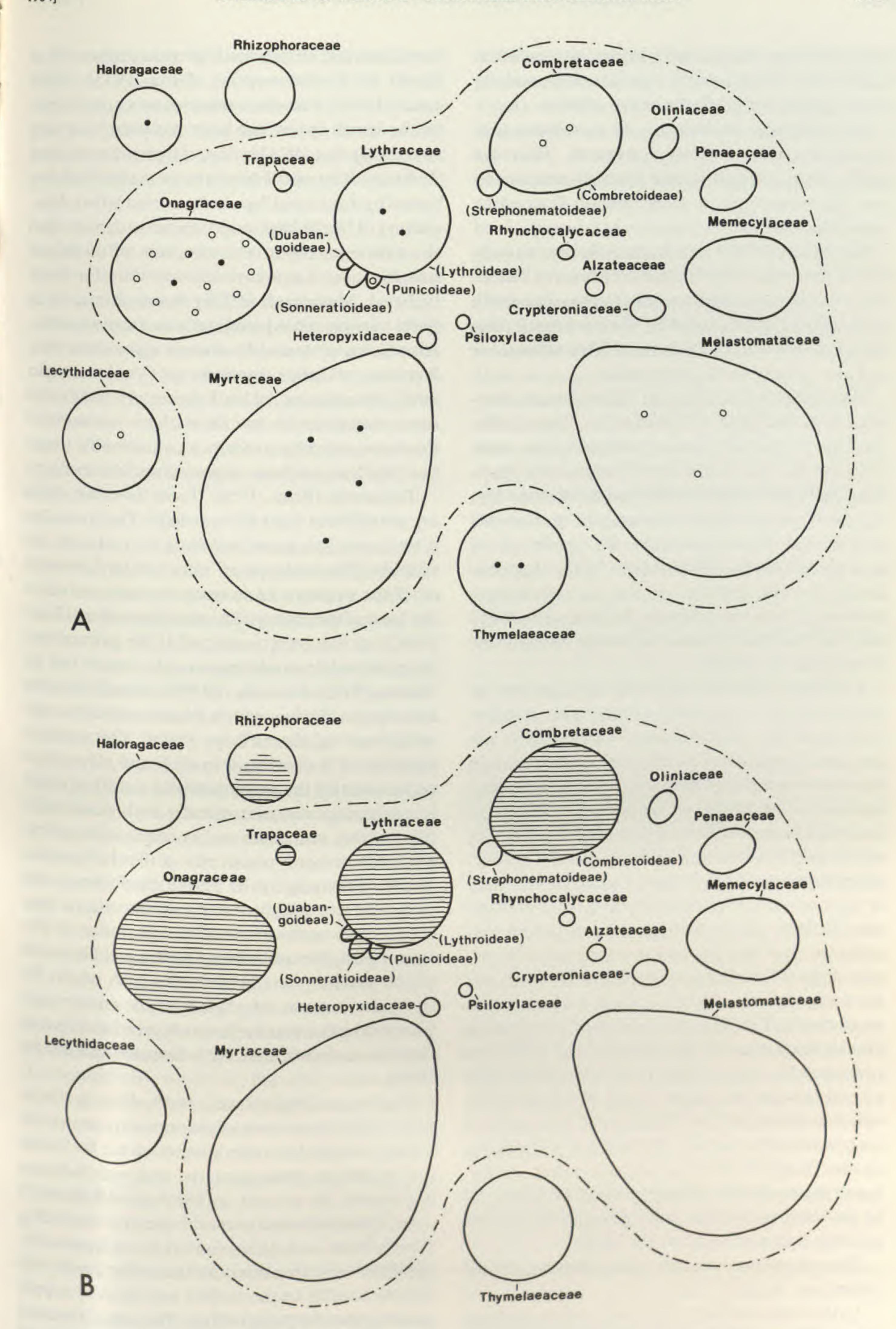
The porate pollen grains of Haloragaceae (see below) and Thymelaeaceae are different and indicate that these families are not allied with the Myrtales.

EMBRYOLOGICAL FEATURES

The main features of embryology of most of the core families of Myrtales, with a number of exceptions mentioned below, are rather uniform (Davis, 1966; Mauritzon, 1939; Schmid, 1984; Schnarf, 1931; Tobe & Raven, 1983a; Wunderlich, 1959). The most extensive presentation of myrtalean embryology is that of Mauritzon (1939). The basic pattern is as follows (see also Table 1 in Schmid, 1984; Tobe & Raven, 1983a):

The anthers are tetrasporangiate, the endothe-

FIGURE 7. Distribution, in the myrtalean and some other families, of:—A. dry (•) and wet (O) stigma types, according to Heslop-Harrison & Shivanna (1977).—B. seed coats with fibrous exotegmen (hatching) according to Corner (1976).



cium develops fibrous thickenings, the tapetum is glandular, cytokinesis is simultaneous, and the pollen grains are bicellular when shed.

The ovules are anatropous, or in various taxa hemianatropous or campylotropous. They are nearly always bitegmic and always crassinucellate. The micropyle is nearly always formed by both integuments.

Mauritzon (1939) noted a peculiarity, namely that in some species of *Combretum* and in *Trapa*, one or both integuments ceased to grow in certain parts, being then replaced by chalazal tissue; this was also observed in *Phaleria* of Thymelaeaceae and also occurs in Myristicaceae.

The integuments of most Myrtales are two-layered at the time of fertilization, but in Oliniaceae, Trapaceae, some Combretaceae, some Onagraceae, and *Cuphea* and *Punica* of Lythraceae, the outer integument consists of more layers. In contrast, both integuments of Lecythidaceae and Rhizophoraceae are made up of several cell layers (Mauritzon, 1939). Lecythidaceae are also peculiar in that the two integuments gradually fuse into one. In Myrtaceae, there may be total fusion into one single integument in a couple of genera.

A primary parietal cell is cut off from the archesporial cell in probably all Myrtales, a difference from the Lecythidaceae, where this is not the case. In addition, at the time of fertilization the nucellus is generally partly intact in the core families of Myrtales, whereas in the genera of Lecythidaceae and Rhizophoraceae studied, the whole nucellus between embryo sac and epidermis is destroyed at this stage. The epidermis may or may not divide periclinally to form a nucellar cap. Embryo-sac formation, with important exceptions (see below), conforms to the Polygonum-type. The synergids are usually hooked, and the antipodals are mostly ephemeral [a fact that according to Tischler (1917) implies a weakening of the basal part of the embryo sac, and thus perhaps a first step leading to the Oenothera-type of embryo-sac formation found in Onagraceae, which lack antipodals]. Endosperm formation is always initially nuclear. Embryogeny conforms to the Onagrad, Asterad (occasionally), or Solanad types. In the mature seed all or nearly all of the endosperm has been consumed and the embryo occupies most of the space.

The exceptions from the above pattern are notable:

Lythraceae conform well to the ordinal pattern of embryology. A uniseriate or, less commonly,

a multiseriate suspensor is present in the embryo (Joshi & Venkateswarlu, 1935a, 1935b, 1936; Joshi, 1939). The occurrence of two nucelli within the same ovule has been reported in several cases (species of Cuphea, Lagerstroemia, and Nesaea). The archesporium is multicellular as noted by Joshi and Venkateswarlu (1936). Mauritzon (1934, 1939) found Cuphea to deviate from the other genera in the structure of ovule and nucellus; also Lagerstroemia was found to be peripheral; Mauritzon (1939) found Punica to be quite similar embryologically to Lagerstroemia. Also Sonneratia and Duabanga agree in the main features to other Lythraceae (Venkateswarlu, 1937; Mauritzon, 1939; Johri et al., 1967). The inner integument in Duabanga increases in thickness apically to form a considerable tissue, but this has not been reported in Sonneratia.

Trapaceae (Ram, 1956; Trela-Sawicka, 1978) are peculiar in their embryology. The ovule has a long nucellar beak and thus no ordinary micropyle. The endosperm may not be formed at all if the primary endosperm nucleus moves to the base of the embryo sac and degenerates (Ram, 1956), or it is very restricted if the primary endosperm nucleus undergoes only one or two divisions (Trela-Sawicka, 1978) to form a few free endosperm nuclei, which degenerate before development of the embryo starts. The nutritive function of the endosperm of Trapa natans L. is taken over by the suspensor and nucellus, which in early stages consist of cells with dense cytoplasm; later, suspensor and nucellus cells undergo endomitotic polyploidization (Trela-Sawicka, 1978). Embryogeny in Trapa conforms to the Solanad-type, and the embryo haustorium is long, coiled, and multiseriate. One cotyledon is also suppressed, the other being fleshy and filled with starch grains (starchy embryos also occur, for example, in some Myrtaceae). The anther tapetum becomes irregularly two-layered and its cells become multinucleate with frequent nuclear fusions.

Oliniaceae (Mauritzon, 1939; Rao & Dahlgren, 1969) have hemianatropous to campylotropous ovules but otherwise conform well with the myrtalean basic pattern, although data are not known for several embryological features.

In Combretaceae several genera, including Combretum and Quisqualis, have plasma-rich, papillate cells that connect the stylar canal with the micropyles of the ovules and seem to supply nutrients to the pollen tubes. Thus they function as an obturator and correspond to the obturator

of Thymelaeaceae. Mauritzon (1939) found tetrasporic, 16-nucleate embryo sacs of the *Peperomia*-type, rather similar to those of the *Penaea*-type (see below), in two species of *Combretum*, but the studies by Fagerlind (1941) on *Quisqualis* and by Venkateswarlu and Prakasa Rao (1972) on several genera, including *Combretum*, showed only monosporic embryo sacs, and it is thus doubtful that tetrasporic embryo sacs occur in this family. The conditions are so interesting that a re-examination would be desirable.

Penaeaceae were studied by Stephens (1909) and consistently seem to have a 16-nucleate tetrasporic embryo sac of the so-called *Penaea*-type. Most often four nuclei fuse in the center and after fertilization result in a 5-ploid endosperm nucleus. The family is rather poorly known embryologically and modern studies are thus very desirable.

According to Tobe and Raven (1984a) the genus Alzatea, composing Alzateaceae, agrees with other Myrtales in the main embryological features, but has a bisporic, Allium-type, embryo sac. Like Rhynchocalyx (Rhynchocalycaceae) but unlike other Myrtales, the micropyle is formed by the inner integument alone. Rhynchocalyx (Tobe & Raven, 1984b) shows the Polygonumtype of embryo sac formation, differing in this characteristic from both Penaeaceae and Alzateaceae. In this respect it exhibits a more basic state than both of these families. Rhynchocalyx differs from the Lythraceae in some respects, including the ephemeral endothecium and the micropyle formed by the inner integument alone (see above), but it agrees with Lythraceae in having a multi-celled archesporium.

Within the three, rather divergent, genera of Crypteroniaceae, Axinandra has so far been studied (Tobe & Raven, 1983b). In this genus the micropyle is formed by both integuments, the archesporium in the ovule is one-celled, and the embryo sac formation is of the Polygonum-type. It is noteworthy, however, that the pollen grains in Axinandra are shed in the tricellular stage, as in the case in several Melastomataceae, and that—unlike all other Myrtaceae studied—it has an endothelium (i.e., an integumentary tapetum) (Tobe & Raven, 1983b).

Melastomataceae deviate from Memecylaceae in having a poorly developed (often crushed) endothecium, whereas Memecylaceae have a thickened, even fibrous endothecium (Davis, 1966; Eyde & Teeri, 1967). The tapetal cells in these families are uninucleate. Although Brewbaker

(1967) reported trinucleate pollen grains in most genera of the family, Tobe and Raven (1984c) report that the grains are strictly 2-celled when dispersed, as is the case in all other families of Myrtales. The placental epidermis may consist of palisade-like cells with a large amount of protoplasm (Subramanyam, 1948), which has also been observed in certain Lythraceae. Subramanyam (1948) also observed that in mature seeds of *Melastoma malabathricum* L. the embryo was filled with starch grains, which is also the case with Trapaceae and some Myrtaceae. Otherwise, the ovular conditions conform well with the ordinal account given above.

Myrtaceae, and in particular 'Metrosiderineae,' agree with the last mentioned three families in embryological attributes (Mauritzon, 1939, and later references). The ovules vary with regard to their position and are often hemianatropous or campylotropous (Johnson & Briggs, pers. comm.). The presumed similarity in flower and fruit morphology between 'Myrtineae' and Lecythidaceae stated by, for example, Niedenzu (1893) was not supported by embryology, as Lecythidaceae are very divergent embryologically (see below). Within Myrtaceae, the micropyle may be formed only by the inner integument (Angophora, Darwinia, Thryptomene, Wehlia) (Davis, 1968, 1969; Prakash, 1969a, 1969b, 1969c), and unitegmic ovules occur in perhaps all species of Syzygium. The archesporial cell has rarely been observed to cut off a parietal cell, but Davis (1966; Prakash, 1969a) suspects that this happens so early that it has usually escaped observation. Adventive embryogeny is reported in the family, and polyembryony is common.

In Onagraceae (Johansen, 1929, 1934; Davis, 1966) the embryo sac formation follows the *Oenothera*-type and is 4-nucleate, the single polar nucleus fusing with a male gamete into a diploid endosperm. In this peculiarity, which seems to be consistent in the family, Onagraceae are well characterized.

Except for certain characteristic features occurring in particular families, of which the *Penaea-* and *Oenothera-*types of embryo-sac formation in Penaeaceae and Onagraceae respectively seem to be the most conspicuous, there is good conformity among the families of Myrtales in embryological characteristics. A most aberrant member is *Trapa*, which, however, seems adapted in its embryological syndrome characteristic of an aquatic life.

Among the families with dubious affinity to

Myrtales, Rhizophoraceae do not deviate considerably from the Myrtales pattern. The antipodals are not ephemeral as they usually are in Myrtales. Any specializations in embryo development (Corner, 1976) of the halophytic mangrove genera seem of little significance in discussing phylogenetic relationships.

Thymelaeaceae are very distinct from Myrtales in embryological respects (Fuchs, 1938; Davis, 1966; Corner, 1976; Tobe & Raven, 1983a). The pollen grains are tricellular when shed (a derived attribute found in Myrtales only in Axinandra, Tobe & Raven, 1984a). As in many Myrtales, however, a parietal cell is cut off from the archesporial cell and forms a parietal tissue, and also a nucellar cap is usually formed by periclinal divisions of the nucellus epidermis, which occurs in certain Myrtales. Unlike most Myrtales, however, the antipodals are persistent. An obturator of elongated cells from the base of the style is characteristic. Similar persistent and proliferated antipodals and a similar obturator occur in Combretaceae.

As regards Haloragaceae (embryological summary by Orchard, 1975), this family must be considered in the strict sense (i.e., excluding Gunnera and Hippuris). In this circumscription, the family yet deviates in embryological respect from Myrtales in some important features. The anther wall formation in both Haloragis and Laurembergia has, for example, proved to be of the monocotyledonous type, although this may not be the case in Myriophyllum, and the pollen grains of all three genera are shed in the tricellular stage. Cellular endosperm formation is recorded in Haloragis (Nijalingappa, 1975) and one species of Myriophyllum but nuclear endosperm formation in another species of Myriophyllum and in Laurembergia. In all three genera mentioned, the embryogeny conforms to the Myriophyllum variation of the Caryophyllad type, which has not yet been found in Myrtales. The combination of attributes does not support the inclusion of Haloragaceae in Myrtales.

Of other families occasionally referred to Myrtales, Hippuridaceae by virtue of the unitegmic ovules with cellular endosperm formation fall out of the pattern. Even more so do Callitrichaceae, which have unitegmic, tenuinucellate ovules, no parietal cell, cellular endosperm formation, and terminal endosperm haustoria (these are totally absent in Myrtales).

Elaeagnaceae are surprisingly poorly known

embryologically, but the evidence known is in accord with the myrtalean pattern.

Lecythidaceae (Venkateswarlu, 1952) deviate strongly from Myrtales, and the pollen grains are sometimes reported to be tricellular when dispersed, which is rare in Myrtales. The ovule is tenuinucellate and no primary parietal cell is cut off from the archesporial cell, which is a difference from Myrtales. Also, the outer integument is thicker in Lecythidaceae than in nearly all Myrtales, and the nucellus becomes destroyed much earlier in the development. Some features, e.g., the ephemeral antipodials, agree with the myrtalean pattern.

The embryological evidence supports the myrtalean core families as related. The seven primary characteristics enumerated by Tobe and Raven (1983a) occur together only rarely in other plants, and in none of the other families that have been referred to Myrtales, with the possible exception of Elaeagnaceae.

SEED COAT STRUCTURES

The seed coat structures in a great number of representatives of dicotyledons were studied by Corner (1976). In a chapter called "Criticism of the arrangement of dicotyledonous families into orders," Corner stressed that the families here considered the core families of Myrtales fall into two groups as follows (Fig. 7B):

(1) seeds with a fibrous exotegmen composed of narrow pitted fibers or elongate tracheid fibers, often with sclerotic mesotesta: Combretaceae, Onagraceae, Lythraceae, Punicaceae, Sonneratiaceae (Punicaceae and Sonneratiaceae are here included in Lythraceae), Trapaceae, Legnotidaceae;

(2) seeds with sclerotic mesotesta but without a special exotegmen: Lecythidaceae, Memecylaceae, Melastomataceae, Myrtaceae, Penaeaceae, Rhizophoraceae (excl. Legnotidaceae).

Haloragaceae lack both sclerotic mesotesta and fibrous exotegmen and thus form a third group, to which also Callitrichaceae were referred (however, a position for Callitrichaceae in or near Myrtales is out of the question).

Corner (1976: 37) incorrectly stated that the first group has tenuinucellate ovules; actually, they are crassinucellate in all the families. The second group, with the exception of Lecythidaceae, likewise has crassinucellate ovules (Lecythidaceae, likewise has crassinucellate ovules (Lecythidaceae being surely out of place in Myrtales).

Another difference between the groups created

by Corner (1976) would be that in the first group the seeds are: "exalbuminous, exarillate and provided with straight or slightly curved embryos. Punica with epidermal sarcotesta seems to provide the least specialized and reduced seed." Starch grains often occur in the embryos of Myrtaceae, but this is not a general feature of the second group. Besides, starch grains occur in the seeds of Trapaceae in the first group. Arils are also generally absent in the second group except for Lecythidaceae, lacking in all Melastomataceae, Myrtaceae, and Penaeaceae and in most but not all genera of Rhizophoraceae. Thus, this is not a difference either. Also the curvature of the embryo comprises no considerable difference between the groups. The sarcostesta in Punica is no doubt a specialization.

Because the difference in seed coat structure was stressed by Corner as important and, together with Corner's other arguments, was used by Briggs and Johnson (1979) as the basis for a distinction between Lythrales and Myrtales, it needs some comment.

In group (1) there is similarity between taxa of the three subfamilies (Lythroideae, Sonneratioideae, and Punicoideae) of Lythraceae studied by Corner in the possession of a multiplicative outer integument ("testa sensu stricto"), the middle layers consisting of either a thin-walled mesophyll or a densely sclerotic part (in Lawsonia and Lagerstroemia with crystals in the cells) or both, or by sclerotic cells only. The innermost layer of the outer integument may contain crystals. The inner integument consists of two layers only, an outer layer of narrow longitudinal tracheids or of narrow thick-walled fibers, and an inner unspecialized layer with elongate thinwalled cells. These observations support the general conclusions that these subfamilies are closely related.

Onagraceae have a non-multiplicative outer integument ("testa") composed of large, often crushed cells, but rarely, as in *Oenothera*, of sclerotic cells. As in some members of the aforementioned families, the innermost layer of the outer integument consists of crystal-cells. The tegmen in Onagraceae, as in the previous families, also remains two-layered. The outer layer consists of longitudinal lignified fibers. Thus, it seems, Onagraceae belong to the first group of families, and in particular resemble some Lythraceae, in seed coat structure.

Combretaceae may or may not have a multi-

plicative outer integument, the mesophyll consisting of thin-walled cells with scattered sclerotic or tracheidal cells with more or less reticulate, in some cases spiral-annular, wall thickenings. The innermost layer of the outer integument is composed of sclerotic or tracheidal cells or is unspecialized. The inner integument consists of an outer layer of elongate, lignified fibers, while the other layers are unspecialized or crushed.

The conditions in group (2), above, are not much different. The outer integument is multiplicative in the large seeds (Memecylaceae) but not in the smaller seeds studied (Melastomataceae). The outer epidermis varies much, from a palisade-like layer of radially elongate cells, as in some families of the former group, to a layer of cuboid cells with thickened outer walls. The mesophyll is thin-walled or there may be groups of sclerotic cells (as in the previous group). The innermost layer of the outer epidermis is unspecialized or (as in some members of the previous group) may consist of crystal-cells. The tegmen is not multiplicative and consists of two celllayers. Unlike the families of the first group the outer layer of the tegmen in the studied taxa does not consist of fibers but is more or less crushed.

In Myrtaceae, the outer integument in the seed may or may not be multiplicative and may or may not develop sclerotic tissue. The innermost layer may or may not consist of crystal-cells, the cell walls in this layer may be thin or thick and lignified, or may even be developed as radially elongate sclerotic cells at the micropylar end. As in group (1), the inner integument is not multiplicative, but mostly unspecialized and crushed; however in *Psidium* the outer layer may have slight, unlignified thickenings.

In the above variation Corner (1976) lays most stress on the occurrence of fibers or tracheids in the exotegmen, i.e., the outermost layer of the inner integument. However, tracheidal cells may be present in the endotesta, i.e., the innermost layer of the outer integument, as in Combretaceae, but not in Lythraceae studied. The presence of sclerotic cells to some extent seems to comprise a typical feature in Myrtales. The several-layered inner integument in Combretaceae is also notable, as is its few-layered outer integument. An evaluation of these differences can be made only in the light of a more complete knowledge of the variation in each family.

A division of Myrtales into two orders was suggested by Corner (1976), largely on the basis

of seed coat structure. The seed coat structures in Myrtales are so divergent, however, that these can hardly be the main basis of such a rearrangement, although the occurrence of a fibrous exotegmen is perhaps important for relating some families to each other and contributes a piece of evidence for including Sonneratiaceae and Punicaceae into Lythraceae. However, the additional characteristics stated by Corner (see above) as differences between the orders have proved inaccurate or only partly true. To the former category belongs the statement that tenuinucellate ovules characterize the Lythraceae group (see above). Development of stamens, occurrence of starch in the embryos, etc., do not provide any differences between the suggested orders. Briggs and Johnson (1979), who accepted a division of Myrtales largely according to Corner's views, subsequently have abandoned this view.

CHLOROPHYLLOUS/ACHLOROPHYLLOUS STATES OF EMBRYO IN SEED

The occurrence of chlorophyllous embryos in seeds was presented by Yakovlev and Zhukova (1980) and discussed by Dahlgren (1980b). Chlorophyll formation in the embryo of seeds normally seems to be dependent on availability of light to the embryo in the course of its development and thus is generally absent in seeds with copious endosperm and in seeds enclosed in a thick testa or pericarp.

In Myrtales, the embryo is usually achlorophyllous despite lack of endosperm. The records in the order are few, however. Chlorophyllous embryos were found in the mangrove genus Laguncularia of Combretaceae, in two species of Memecylon of Memecylaceae, in Sonneratia of Lythraceae, and in two species of "Eugenia" (= Syzygium) of Myrtaceae. The records of achlorophyllous embryos are distributed through the order and include all families investigated except Memecylaceae. No taxonomic conclusions can as yet be drawn on the basis of this feature. The few studied taxa of Haloragaceae and Thymelaeaceae have achlorophyllous embryos, in which they agree with most Myrtales.

CHROMOSOME NUMBERS

Raven (1975) gives a summary of the chromosome numbers for the Myrtales. He concludes that as the base number is X = 12 in Trapaceae, Oliniaceae, and Combretaceae, and as this num-

ber has also been reported for both Psiloxylaceae and Heteropyxidaceae (Johnson & Briggs, 1984), it is likely to be the original basic number for the order as a whole (or, less plausibly, X = 11, which Raven assumed to be the original base number in Myrtaceae and Onagraceae).

Onagraceae (Raven, 1975) have X = 11, which is found in Fuchsieae and Circaeeae and in the more primitive taxa of Lopezieae and Onagreae.

Trapa (Trapaceae) has X = 12.

Within the Lythraceae, Lafoënsia has a chromosome number of n = 10, Lagerstroemia n = 22-25, Lythrum n = 5, Heimia n = 8, Nesaea n = 30, Peplis n = 5, Rotala n = 16, Woodfordia n = 8, and Cuphea n = 6, 8, or 9, which suggests a basic number of the family of X = 8. This also seems to be the basic number in other genera not mentioned here (Graham, pers. comm. in Raven, 1975). Punica, as most other Lythraceae, has n = 8, while Duabanga has X = 12 and Sonneratia X = 9 or 11 (Muller & Hou-Lin, 1966).

Penaeaceae (Dahlgren, 1968, 1971) have n = 10, as in *Rhynchocalyx* (Goldblatt, 1976). The chromosome numbers in Crypteroniaceae, as circumscribed here, are not known. In Memecylaceae, *Memecylon* has X = 7 and *Mouriri* (one count only) n = 12, whereas several genera of Melastomataceae have basic numbers of X = 14, 12, and 9. Oliniaceae and Combretaceae, which show some other similarities, both are reported to have the basic chromosome number of X = 12.

Thymelaeaceae have a probable base number of X = 9. Finally, Haloragaceae (excl. Gunnera and Hippuris) have X = 7, Rhizophoraceae n = 32 (tribe Macarisieae) and n = 18 (tribe Rhizophoreae), suggesting base numbers of X = 8 and 9; whereas, the base number of Lecythidaceae may be difficult to establish, n = 13, 16, 17, and 18 being some numbers reported in that family. Chrysobalanaceae have n = 10 or (more often) 11. Finally, it may be mentioned that Rhamnaceae have a base number of X = 12, with X = 11 in the tribe Colletieae (Raven, 1975).

The chromosome base numbers of the Myrtales, as compared with those in other families, do not support inclusion of Lecythidaceae in the order (rather Lecythidaceae fit with the Theales), though Rhamnaceae agree better (X = 12 being, however, a base number in many complexes).

CHEMICAL CHARACTERISTICS

Myrtales, as circumscribed here, comprise a fairly homogenous complex in terms of chemical contents (Hegnauer, 1964, 1966, 1969, 1973).

Tannins. All families of Myrtales appear to contain tannin plants. In most of the families the tannins consist of the condensed type as well as of galli- and ellagi-tannins. Ellagic acid, according to Bate-Smith (1962), occurs in all studied taxa of Lythraceae (incl. Punicaceae), Combretaceae, Melastomataceae, Myrtaceae, and Onagraceae and, according to Lowry (1976), in Lythraceae subfam. Sonneratioideae; probably it is present in virtually all members of the Myrtales. Even a water plant like Trapa is known to be rich in tannins, the pericarp containing up to ten percent or more (Gnamm, 1949)! Species of Combretaceae, which are rich in gallyol- and ellagi-tannins as well as condensed tannins, are used for tanning.

Hegnauer (1969) concluded that "gallic and ellagic acids and tannins derived from these, as well as condensed tannins which are derived from flavon-3-oles and flavon-3,4-dioles, are characteristic of the order Myrtales."

Tannins are also present in rich quantities in Rhizophoraceae. Bate-Smith (1962) recorded small quantities of ellagic acid in Cassipourea, but not in Rhizophora; whereas Lowry (1976) reported ellagic acid in species of Anisophyllea and Bruguiera as well as in Rhizophora. In Haloragaceae ellagic acid has been reported (Bate-Smith, 1962) for Haloragis as well as Myriophyllum, in Elaeagnaceae for Elaeagnus and Hippophaë, and in Lecythidaceae for Couropita, Eschweilera, and Lecythis. All these groups are tannin plants in the wide sense. Thymelaeaceae, however, consistently seem to lack ellagic acid and accumulate no tannins, an important difference from all Myrtales.

Flavonoids. The flavonoid profile (Bate-Smith, 1962; Gornall et al., 1979) in Myrtales is based mainly on common flavonols and their O-methyl derivatives (e.g., delphinidin, cyanidin, pelargonidin, quercetin, kaempferol, O-methylated anthocyanins, and, quite often, proanthocyanidins). The methylated and oxygenated flavonols are especially common in Combretaceae. Myricetin occurs in some families (at least in certain genera of Combretaceae, Melastomataceae, Myrtaceae, and Onagraceae), but is of much rarer occurrence than are ellagic acid and quercetin. Glycoflavones are reported in at least single genera of each of the Lythraceae, Combretaceae, and Myrtaceae, and occur in all tribes except Onagreae and Epilobieae of the Onagraceae (Averett & Raven, 1983). In fact, glycoflavones may be widespread in Myrtales. Flavones are noticeably poor in the order. Caffeic

acid is also rare in the order, except in Onagraceae (Bate-Smith, 1962).

The flavonoid pattern for Thymelaeaceae (Gornall et al., 1979) is different from that in Myrtales. Methylated flavones, C-glycoflavones, and luteolin/apigenin are reported, whereas delphinidin, cyanidin, pelargonidin, O-methylated anthocyanins, and myricetin are *not* recorded.

Rhizophoraceae are known to possess cyanidin/pelargonidin, myricetin, quercetin/kaempferol, and proanthocyanidins, and thus agree rather well with the myrtalean profile. Also Haloragaceae agree with Myrtales in flavonoid profile and, like Rhizophoraceae, seem to lack or be poor in flavones, as are Myrtales. In addition, Myrtales agree fairly well with Theales, Rosales, and other orders, such as Geraniales and Balsaminales, in flavonoid contents.

Essential oils. Myrtaceae are the only family in Myrtales with rich production of essential oils. The essential constituents of these (Penfold, 1948) in many cases are monoterpenes and, often to a considerable proportion, sesquiterpenes. Oils of phenyl-propane type are rarer. Characteristic of myrtaceous oils are phloroglusin derivatives of the baeckeol, eugenin, and tasmonol types.

Essential oils are also present in flowers of Lawsonia (henna plant) of Lythraceae.

Although Thymelaeaceae are not essential-oil plants, and lack ducts, the wood of some taxa contains essential oils.

Triterpenes; triterpene saponins. Triterpenes are widely distributed throughout the order Myrtales, and triterpene saponins are recorded from Combretaceae and Myrtaceae, although they are rare in the latter family. The occurrence of triterpene saponins in the other core families of Myrtales is uncertain or, at least, not common.

It is noticeable that the saponin barringtogenol has been recorded in Combretaceae and Barringtonia (of Lecythidaceae sensu lato) only, but the phylogenetic significance of this condition is uncertain.

Triterpene saponins are also known to occur in *Haloragis* of Haloragaceae, and richly so in the fruits of *Shepherdia* of Elaeagnaceae, but also in some Thymelaeaceae.

Cyanogenesis. Cyanogenic compounds occur in several families of the Myrtales, viz., in Memecylaceae (Memecylon), Myrtaceae (Eucalyptus), Lythraceae (Lawsonia), and Onagraceae (Gaura, Oenothera). Besides, wounded parts of Olinia (Oliniaceae) are reported to smell like "bitter almonds," indicating cyanogenic compounds related to prunasin. Cyanogenic compounds are also known in Haloragaceae (Haloragis and Myriophyllum).

Alkaloids. Alkaloids are scattered in Myrtales and are reported in the families Combretaceae, Lythraceae (incl. Punica), Melastomataceae, and Myrtaceae. Although alkaloids have also been reported sporadically in Onagraceae, their presence has not been confirmed and the report is most likely incorrect.

Within Combretaceae the genus Quisqualis seems to contain a pyridin base. Lythraceae are richer in alkaloids and produce an interesting type of quinolizidine alkaloids not known from any other plants (Fujita et al., 1971; Seigler, 1977). Punica produces alkaloids similar to the better known tropane types, the chief being isopelletrierin, N-methylisopelletrierin, and pseudopelletrierin (Hegnauer, 1969), while others remain to be identified. Positive alkaloid reactions have been obtained for the genera Memecylon (Memecylaceae) and Clidemia and Sonerila (Melastomataceae), but these alkaloids have not been isolated. Alkaloids are rare in Myrtaceae, but alkaloid reactions have been obtained for a number of genera; they await further analysis.

Among other families associated with Myrtales, Rhizophoraceae are characterized by their alkaloids, which include hygrolintropine, and pyrrolizidin (necine) derivatives. Some of the alkaloids contain sulfur.

Haloragaceae seem to be alkaloid-free or almost so (Orchard, 1975), while Elaeagnaceae contain tryptofan derivatives (Boit, 1961) such as elaeagnin and serotonin. Alkaloids are rare and little known in Thymelaeaceae.

There does not seem to be a consistent tendency in the alkaloid contents of the myrtalean and "possibly-myrtalean" families; the alkaloid contents in several families still largely remain to be analyzed.

Quinones. Napthaquinones are known to occur in some taxa of Myrtales. The napthaquinone lawsone is known in Lawsonia of Lythraceae (also in Impatiens of Balsaminaceae). Lawsone accounts for the color in henna, which is used for dyeing hair and nails. Quinones (of unknown structure) are also known in Dichaetanthera of Melastomataceae (Hegnauer, 1969).

Anthraquinones are known in Sonneratia (Lythraceae). The occurrence of quinones thus offers no taxonomically useful information.

Aluminum accumulation. Aluminum accumulation (Chenery, 1948) is noticeable in Crypteroniaceae (Crypteronia) and especially in

Melastomataceae and Memecylaceae (more than 10,000 p.p.m. in several genera). Aluminum accumulation occurs also in Rhizophoraceae subfam. Anisophylleoideae (*Anisophyllea, Combretocarpus*, and *Poga*), but not in the other rhizophoraceous subfamilies (Chenery, 1948; Chenery & Sporne, 1976).

Mucilage. Mucilage cells characterize some families of Myrtales, viz., Combretaceae, Lythraceae, and Melastomataceae (quite often, Hegnauer, 1969). The mucilage contains sugars and is often acid in reaction.

Storage substances in the seed. The seeds of myrtalean families mostly have a large and well-developed embryo, whereas the endosperm tissue is absorbed in the course of the seed development. Therefore, we are chiefly concerned here with the contents of the embryo. In most families, the embryo stores fatty oils and proteins, but it sometimes stores starch in Melastomataceae and Myrtaceae and always does in Trapaceae. Endosperm may be present or absent in Rhizophoraceae. If the latter, the embryo is large and stores fat and protein, which is also true in most Lecythidaceae, Thymelaeaceae, Elaeagnaceae, and Haloragaceae.

Phytochemical summary. Hegnauer (1969: 195), in a somewhat resigned comment, summarizes: "One must frankly admit that so far chemistry cannot give a decisive contribution to the problem of the descent of the Myrtales. Similar polyphenolic and triterpene spectra occur in the Cunoniales, Theales, Rosales, and Myrtales."

The families of Myrtales lack polyacetylenes, iridoid substances, and benzylisoquinolin alkaloids. The occurrence of such compounds in any taxon referred to the Myrtales indicates against inclusion of that group in the order.

The presence of tannins, both galli- and ellagitannins and tannins of the condensed type, is typical of the order, and the flavonoid spectrum is characterized by the presence of flavonols (including methylated flavonols), whereas, flavones (except glycoflavones) are absent or nearly so in the families studied. Triterpenes are characteristically present, and triterpene saponins are found in various representatives. Alkaloids occur sporadically in the order but show no consistent pattern. Napthaquinones are known in different subfamilies of Lythraceae. Mucilage cells with polysaccharide contents are common but not a criterion of Myrtales. Cyanogenesis occurs in several families, but again does not represent a typical attribute of the order. Considerable aluminum accumulation occurs in Crypteroniaceae, Memecylaceae, and Melastomataceae and may indicate affinity among these families, but this affinity is better shown by other attributes. The seeds have but little endosperm and their embryos usually accumulate fat and aleuron, exceptions being some Myrtaceae and Melastomataceae and the Trapaceae which store starch; this character is obviously of little phylogenetic significance. Myrtaceae, Heteropyxidaceae, and Psiloxylaceae deviate from the other families in their rich contents of essential oils.

The possession in Thymelaeaceae of poisonous compounds, coumarins of the daphnetic and daphnoretin type, and the lack of tannins and ellagic acid are strong indications that this family should *not* be associated with Myrtales, but that it may have close relationship with the Euphorbiaceae.

Rhizophoraceae agree rather well with Myrtales in the main chemical features, although the alkaloids present in subfam. Rhizophoroideae are absent from Myrtales. Otherwise the tannin content (incl. ellagi-tannins), flavonoid spectrum, mucilage cells, aluminum accumulation, and oilrich seeds are in agreement with myrtalean families, and Rhizophoraceae cannot be separated from this order on chemical grounds.

Also Haloragaceae (excl. Gunnera and Hip-puris) show a similar pattern; ellagic acid, quercetin, kaempferol, etc. are typical. Saponins and cyanogenic compounds found in the family are also present in Myrtales.

Lecythidaceae, which are often saponin-rich (triterpene saponins), agree fairly well with Myrtales in chemistry, but similar chemistry occurs in Theales; hence, the position of the family does not become obvious from chemistry.

Elaeagnaceae agree with the myrtalean families in general chemical features but the accumulation of L-quebrachite and the tendency for accumulation of indole bases and of sinapinic acid are *not* in accordance with Myrtales (Hegnauer, 1966).

By their possession of iridoids in at least some genera the families Escalloniaceae (or Escallonioideae of Saxifragaceae), Icacinaceae, Hippuridaceae, Loganiaceae, and Callitrichaceae are deemed distantly related to Myrtales.

THE CORE FAMILIES OF MYRTALES

Myrtales, like Caryophyllales (or Chenopodiales), are one of the few larger orders that have

a rather uncontroversial circumscription as regards the "nucleus" or "core" families. These are the Onagraceae, Trapaceae, Lythraceae (incl. Punicaceae and Sonneratiaceae), Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, Melastomataceae, Psiloxylaceae, Heteropyxidaceae, and Myrtaceae. All of these entities may not necessarily be entitled to familial status, but in essential points this does not make a great difference. (See p. 635 for the preferred classifications of each of the two authors.)

ONAGRACEAE A. L. DE JUSSIEU (1789)

This family has 17 genera and ca. 675 species (Raven, 1964, 1976, 1979), ranging from the tropics to (especially in Epilobium) arctic-alpine habitats. Through the works of Munz, Raven, and associates, the family has become one of the most thoroughly investigated among the angiosperms. Although most genera are herbaceous, some are woody, and the leaves are opposite, alternate or, more rarely, verticillate, and in some tribes have minute stipules (Fig. 2A-E). The leaf teeth are of the fuchsioid (a variant of rosoid) kind (Hickey, 1981). The vegetative parts are rich in oxalate raphides, which is another unusual feature in the Myrtales. The flowers are epigynous, generally 4-merous, but 2-merous in Circaea and to 7-merous in species of Ludwigia, 5-mery occurring also within several genera (Eyde, 1977). The flowers are provided with a variably long hypanthium (lacking in Ludwigia, Lopezia, and sporadically in other genera). There are generally two staminal whorls or, by reduction, a single whorl in the flowers. By dislocation in the bud, these often appear to be in an obdiplostemonous position although the initials show a diplostemonous organization. Weak zygomorphy occurs in Epilobium (Chamaenerion), Clarkia, and Heterogaura, and strong zygomorphy in Lopezia. The reproductive biology (Raven, 1979) is varied, bird-pollination occurring in most species of Fuchsia and some species of Lopezia, Oenothera, and Epilobium. The pollen grains may cohere in tetrads (Skvarla et al., 1975) and are generally conspicuously triangular and angulo-aperturate. They have various patterns of exine stratification (Skvarla et al., 1976). Most conspicuously they have viscin threads in all but one species (Circaea alpina L.; Skvarla et al., 1978), the last mentioned feature matched only in certain Ericaceae and Fabaceae. Pseudocolpi

are lacking. The carpels (and locules) are generally isomerous with the perianth whorls; in certain taxa the septa are incomplete in the upper part of the ovary. The ovules are usually numerous, and in most features have a myrtalean embryological pattern, although they are conspicuously distinct in having the monosporic, 4-nucleate Oenothera-type embryo sac formation. Antipodals are lacking, and the endosperm is diploid. The fruit in most genera is a loculicidal capsule, but may be a berry (Fuchsia) or an indehiscent dry fruit (Circaea, Gaura, etc.) with a variable number of seeds. The seeds in the tribe Epilobieae are generally provided with a tuft of trichomes and have a taxonomically useful surface sculpture. The embryo lacks starch grains.

Eyde (1981) provides strong evidence that epigyny has evolved separately in two lines within the onagraceous ancestors: in one line leading to *Ludwigia*, which has nectaries on the ovary summit, and one line leading to the other Onagraceae, which have nectaries on the tube side of the gynoecium-tube junction. Differences in vasculature and other details support this conclusion (Eyde, 1981).

The Onagraceae are a very distinctive family, and differ from other Myrtales in several features. The similarities to Lythraceae in teeth structure and marginal ciliation of leaves pointed out by Hickey (1981), and the fibrous exotegmen of the seeds and the similar petal venation are some other conspicuous attributes which may indicate a quite close connection between the Onagraceae and Lythraceae.

TRAPACEAE DUMORTIER (1829)

This family consists only of the genus Trapa, which, excluding introductions, currently has a temperate to tropical Old World distribution. The number of species is perhaps three, although as many as 30 self-pollinating races have sometimes been considered as species. The plants are floating aquatic herbs with decussate leaves, concentrated in rosettes on the branch ends; the leaves are caducous and replaced on the submersed stems by chlorophyllous roots. The stems have bicollateral vascular bundles and the leaves rudimentary stipules, supporting a myrtalean affinity. The floating leaves have marginal teeth with a unique double apex. The flowers are axillary, bisexual and perigynous to hemi-epigynous, with four valvate sepal lobes, four white petals, and four stamens alternating with the petals. The pollen grains are triangular, and have three meridional ridges. They can be interpreted as possessing intercolpate depressions. The ovary is bilocular with one pendulous ovule in each locule, but only one ovule develops into a seed. The family has a unique embryology: the embryo sac formation follows the normal type, but endosperm formation hardly takes place at all. The embryo sac becomes prolonged, and copious nutrient tissue including starch grains are accumulated in the embryo, which has one large and one rudimentary cotyledon.

The family has often been included in Onagraceae, but it lacks the viscin threads on the pollen grains, epigynous flowers, and the 4-nuclear *Oenothera*-type embryo sac of that family. Rather, it seems more closely related to the Lythraceae, although there is no obvious link between the two families.

LYTHRACEAE JAUME ST.-HILAIRE (1805)

This family, with ca. 29 genera and ca. 585 species (see Shaw, 1973; Schmid, 1980; Cronquist, 1981) is here more widely circumscribed, including Punicaceae Horan. as well as Sonneratiaceae Engl. & Gilg. It is widespread and occurs in various climatic zones of the New and Old World, with a concentration in the tropical and subtropical regions. Its new circumscription makes it rather vaguely defined, the newly included genera having epigynous flowers and stamens attached on the inside of the hypanthium or on its rim. With various of its genera it possesses a combination of features that are regarded as basic (plesiomorphic) in the order, in which it takes a central position. The amplitude of variation is considerable.

The family includes herbs and shrubs as well as fairly large trees (Lagerstroemia, Lafoënsia, Sonneratia, Duabanga). The leaves are opposite, more rarely disjunct-opposite, or verticillate, and the leaves are entire or sometimes indistinctly dentate ("cryptic teeth"). The stipules show advancement through their dissection into small trichome-like structures displaced into the leaf axil (see Diplusodon, Fig. 8C).

Branched foliar sclereids are absent in most Lythraceae; they are reported to occur only in Sonneratia and Duabanga. Unbranched sclereids occur rarely in other genera.

The flowers are usually actinomorphic, but in Cuphea and Pleurophora are zygomorphic; Woodfordia approaches this condition. Epigy-

nous or hemi-epigynous flowers occur in Sonneratia, Duabanga, and Punica, but not in the subfamily Lythroideae. The flowers in Lythraceae exhibit a variety of merous conditions: 4-, 5-, or 6-mery being the most common (but to 16-mery occurs in Lafoënsia, to 9-mery in Lagerstroemia, and to 8-mery in Punica and Sonneratia). The flowers possess black glands in Adenaria, Pehria, Pemphis, and Woodfordia. The calyx-lobes are valvate. One pecularity that occurs in a considerable number of genera, incl. Lythrum, Nesaea, Rotala, and Diplusodon (Fig. 8G), is the presence of tooth- and spur-shaped structures isomerous and alternating with the often shorter calyx-lobes; these are nothing but extensions from the calyx-lobe base (and should not be confused with an outer whorl of perianth members), and no doubt can be regarded as a specialization (sometimes secondarily lost). The petals in Lythraceae have a peculiar, pinnate venation, a feature which Chrtek (1969) regarded as a derived attribute, but which has its counterpart in Onagraceae (and thus may be a synapomorphy for the two families). Petals are sometimes absent through reduction and vary widely in relative size and in color (though being usually crimson, pink, or white). When present they are often unguiculate and may be reminiscent of petals in Malpighiaceae in the crinkled, undulate structures.

Stamens more than double the number of sepals are found in Punica and Sonneratia, but also in Lagerstroemia and species of Diplusodon, Ginoria, Heitia, Heimia, Nesaea, and Physocalymma. In haplostemonous flowers the stamens may alternate with the sepals, as in Tetrataxis (Graham & Lorence, 1978) and species of Nesaea (Graham, 1977), or may be opposite to them, as in other species of Nesaea and in species of Rotala, Peplis, Ammannia, and Lythrum. Two stamens or only one are found in species of Rotala and two or four stamens in Didiplis diandra Wood. The filaments are straight or incurved (the long filaments in Lafoënsia inrolled) in bud, and are usually inserted on the inside of the receptacle between its base and middle, closer to the rim in Lawsonia, on the distal inner side of the hypanthium in Punica, and near or on the very rim in some advanced species of Cuphea and in Sonneratia and Duabanga. (The last condition is typical of nearly all other Myrtales except some Combretaceae.) The anthers generally lack strong specialization, and the connective is less developed than in Crypteroniaceae, Penaeaceae, Memecylaceae, or Melastomataceae, but have a broad connective in several woody genera (Capuronia, Lawsonia, Orias, and Lagerstroemia).

The pollen grains are exceptionally variable for the order and include heterocolpate types with pseudocolpi either isomerous to or double the number of the apertures as well as colporate or porate types without pseudocolpi. Porate pollen grains occur in *Cuphea* (Graham & Graham, 1971).

The common division of Lythraceae subfam. Lythroideae is according to whether the ovary is more or less completely septate (Nesaeeae) as is the case in subfam. Punicoideae and Sonneratioideae, or whether the septa are incomplete in the upper part of the ovary (Lythreae). The embryology of Lythraceae is of the common type compatible with the family's basic position in the order. The fruit is capsular or baccate, the seed of *Punica* deviating by its sarcotesta.

(Much of the above, detailed information has been received from A. Graham & S. Graham.)

Punicaceae Horaninow (1834) has been included here, as a subfamily of the Lythraceae. It consists of Punica with two species, P. granatum in southern Europe and western Asia, and P. protopunica Balf. f. on Socotra [this latter species has been placed in the segregate genus Socotria by Levin (1980)]. The fairly large, bright red flowers are epigynous, 5-8-merous in calyx and corolla, and provided with numerous stamens, the filaments of which are attached to the inner side of the hypanthial tube. The stamens develop in centrifugal succession as in Lagerstroemia. The carpels are 7-15 and in P. granatum are situated on two levels, but in P. protopunica form an ordinary syncarpous ovary. The fruit has a leathery pericarp and the seeds are pulpy from the edible sarcotesta. Punica is technically easy to separate as a family, Punicaceae, and is usually treated on the family level.

Also Sonneratia and Duabanga are generally separated, together, as the family Sonneratiaceae Engl. & Gilg, with perhaps ten species. Sonneratia consists of mangrove trees, Duabanga of lowland forest trees. They differ from the Lythraceae in having branched foliar sclereids, and the flowers are hemi-epigynous, relatively large, and have a carnose hypanthium and calyx. Unlike other Lythraceae with numerous stamens, those in Sonneratia seem to develop centripetally. The pollen grains (Muller, 1969) do not possess any distinct pseudocolpi (although their outline may approach a "heterocolpate" type);

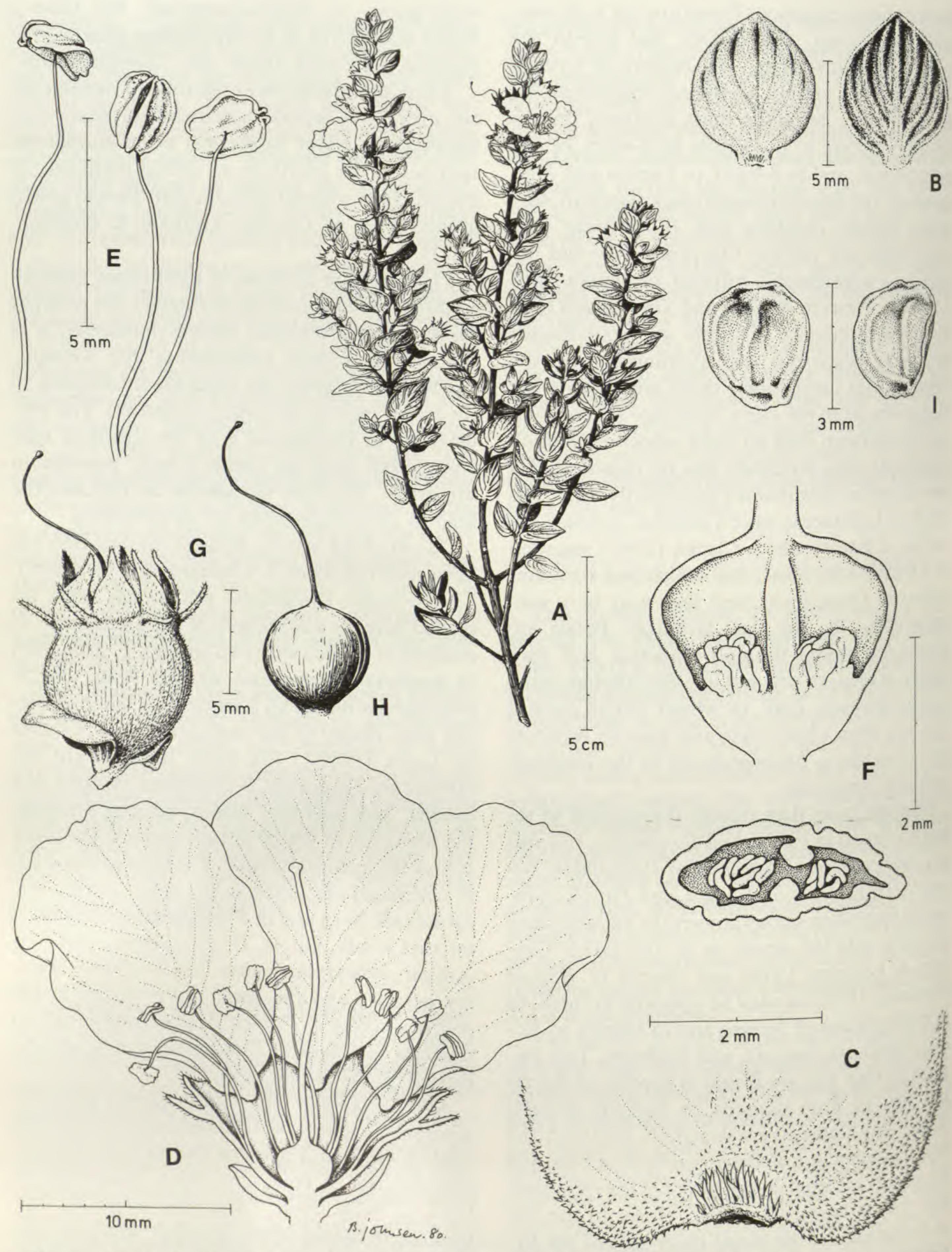


FIGURE 8. Diplusodon sigillatus Lourt. (Irwin et al. 12447 from Brazil).—A. branch.—B. leaf, upper and lower side (left and right respectively).—C. leaf base showing axillary stipules.—D. flower, longitudinal section, note that the petals are inserted on hypanthium rim and have a basal adaxial "knee."—E. stamens in different views.—F. ovary in longitudinal and transversal section.—G. calyx in fruiting stage, showing processes from calyx lobe bases (see text).—H. fruit.—I. seeds. (Orig., del. B. Johnsen.)

they are porate, as in some other Lythraceae, e.g., Diplusodon.

The two genera differ from each other in a number of characters, and it seems questionable whether they are closely enough related to be treated together in the same subfamily. The difference in wood anatomy, demonstrated by van Vliet and Baas (1984); the different chromosome number; the different inflorescence type and fruit, etc., indicate that they are not particularly closely allied and some of the similarities that have been used to justify the previous family, Sonneratiaceae, are likely to depend on convergence. We suggest that each of them be treated as a subfamily (Sonneratioideae, Duabangoideae) under Lythraceae.

Also the genus *Rhynchocalyx*, treated below in the family Rhynchocalycaceae (see below), is often included in Lythraceae.

OLINIACEAE ARNOTT EX SONDER IN HARVEY & SONDER (1862)

This family consists of a single genus, Olinia, with perhaps eight or ten species (Rao & Dahlgren, 1969), of trees with opposite leaves, small stipules (Weberling, 1963), and unicellular hairs. The inflorescence is paniculate, with the branches ending as cymules of three flowers. Each flower is basally subtended by a short internode ending with some blunt teeth, a "calyculus," which is a stem structure. The flowers are epigynous, 4-5merous (Fig. 9E), and have a tubular hypanthium continuing beyond the ovary. On the rim of this hypanthium are four or five elongate white lobes, which probably represent the calyx, and, inside these, and filling up most of the hypanthial mouth, are five thick, incurved, scale-like structures, which are best interpreted as petals. Below these, and inserted on the upper part of the hypanthial tube are the 4-5 isomerous stamens. The stamens, which are thus antepetalous, have a short filament and an anther with a carnose central connective and downwardly directed microsporangia (Fig. 9G). The pollen grains are heterocolpate, but the pseudocolpi are visible only on one hemisphere of the pollen grain (Patel et al., 1984). The inferior ovary is 2-5-locular with axile placentae. The style is short, and in our material the stigma reaches the level of the anthers.

Whether the flowers are self-pollinated or not deserves study. The embryology contributes no exceptional details, and the embryo sac, contrary

to that in Penaeaceae, is monosporic and 8-nucleate. The fruit is drupaceous, and the cotyledons are spirally twisted.

The family approaches, in various respects, Combretaceae, Penaeaceae, Rhynchocalycaceae, Alzateaceae, and Lythraceae sensu lato, but is sufficiently different from all to be regarded as a distinct family. The interpretation of the "scales" as petals makes the flower correspond with Penaeaceae, where the stamens are alternisepalous, and Rhynchocalycaceae, where small petals alternate with the sepal lobes and are situated as hoods next to the stamens (in a fashion reminiscent of certain Rhamnaceae). Oliniaceae resemble the Combretaceae in chromosome number (X = 12), epigyny, and certain other details (see p. 682).

COMBRETACEAE R. BROWN (1810)

This family of ca. 20 genera and 400 species, occurring both in the Old and the New World, and particularly common in subtropical and tropical Africa, consists of trees, shrubs, and lianas, including mangroves, with alternate, opposite, or verticillate leaves lacking stipules or with minute stipules which are displaced into the leaf axils and dissected into multicellular glandular hairs (some species of Terminalia and Buchenavia). The stomata are anomocytic except in Laguncularia and Lumnitzera, where they are cyclocytic (Stace, pers. comm.). The trichomes consist of club-shaped or peltate glandular hairs and of nonglandular hairs which are of a distinctive type ("combretaceous hairs" of Stace, 1965, 1980). The inflorescences may be terminal on branchlets, as well as axillary, and consist of racemes, spikes, or heads with small or mediumsized, epigynous flowers with a usually fairly short hypanthium (sometimes absent or in Quisqualis to 8 cm long). This bears on its rim 4-5(-8) sepal lobes and equally many, mostly rather small petals, which are often lacking, as in Pteleopsis (Fig. 10). There are one or two staminal whorls, the outer sometimes having two or three times the normal number of stamens. The filaments are often long and colored, as may also be the whole flowers, and are inflexed in bud; and the anthers only rarely (Thiloa) have a "massive," fleshy connective. As in several related families, the pollen grains possess pseudocolpi (absent in Strephonema) and are tricolporate or triporate. A well-developed intrastaminal disc is very often

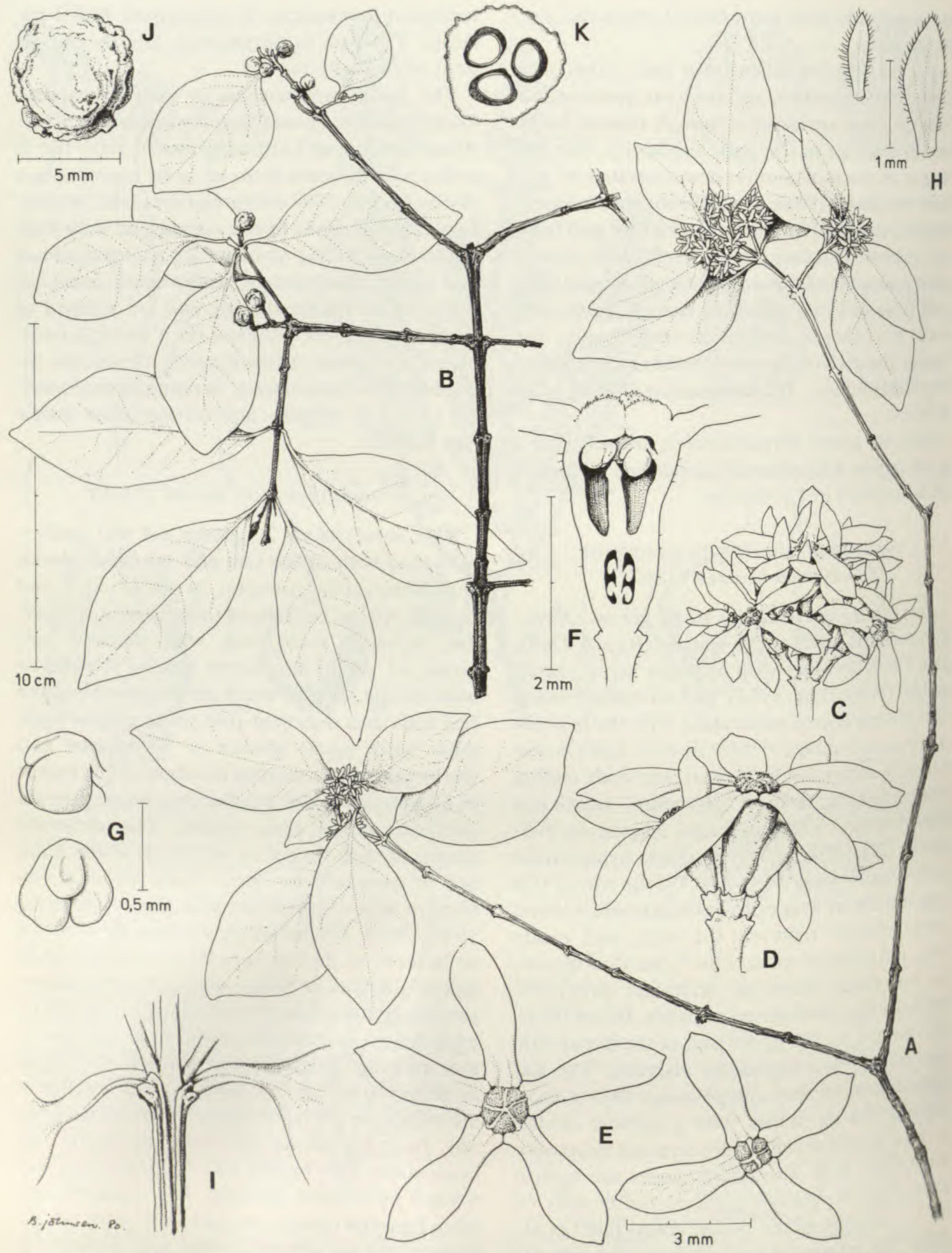


FIGURE 9. Olinia aequipetala (Delile) Cufad. (Oliniaceae), from collections made in Ethiopida: A, C-I. Friis et al. 532; B, J-K. Friis et al. 1228.—A. flowering branch.—B. fruiting branch.—C. inflorescence (panicle).—D. floral triad.—E. penta- and tetramerous flowers seen from above, showing elongate sepals and small papillate petals in hypanthial mouth.—F. flower, longitudinal section.—G. stamens, lateral and adaxial view.—H. caducous bracts.—I. leaf bases with auricles of stem lists.—J. drupe.—K. same in transverse section. (Orig., del. B. Johnsen.)

present. The mostly inferior ovary is 2-5-carpellate and unilocular, with 2(-6) pendulous ovules. An obturator tissue resembling that in Thymelaeaceae is sometimes present, which has been one reason for a suggested relationship between the two families. The embryology otherwise seems to be more or less of the basic myrtalean type [the occurrence of 4-sporic, 16-nucleate embryo sacs described by Mauritzon (1939) needs to be verified]. The fruit is generally one-seeded and indehiscent, rarely dehiscent; it is mostly leathery or drupaceous and often provided with conspicuous wings or ribs.

The family is dominated by the large genera Combretum and Terminalia; species of Laguncularia and Lumnitzera are mangrove trees; and Quisqualis species are creepers. The family is most closely related to those already described, but any close connections are not obvious.

This account of Combretaceae does not include Strephonema, which is a tropical, West African genus with three species. It was treated as a separate family, Strephonemataceae, by Venkateswarlu and Prakasa Rao (1971) on the basis of morphological, embryological (Tobe & Raven, pers. comm.), and anatomical differences from the other Combretaceae, but it is better treated as a subfamily of Combretaceae. The wood-anatomical differences include dimensions of vessels and fibers, the presence of fibertracheids, etc. (see also den Outer & Fundter, 1976, and van Vliet & Baas, 1984). The stomata are paracytic in Strephonema whereas they are anomocytic or cyclocytic in other Combretaceae (Stace, pers. comm.), but its species have the same type of characteristic ("combretaceous") hairs as have other Combretaceae. The flowers are actinomorphic, 5-merous, bisexual, petaliferous, and diplostemonous, and have a half-inferior ovary (inferior in other Combretaceae). The pollen grains lack pseudocolpi. The ovary is unilocular and has two pendulous ovules as in other family members. On the other hand, the massive, hemispheric cotyledons in the seeds of Strephonema contrast conspicuously with the folded, spirally twisted ones in other Combretaceae.

Thus, although fairly distinct, Strephonema is still considered a member of Combretaceae by most taxonomists, e.g., by Exell (1930), Exell and Stace (1966), and van Vliet (1979), who have a profound knowledge of the family. We agree with these authors that the genus should be placed in the Combretaceae family as a separate subfamily, Strephonematoideae.

ALZATEACEAE S. GRAHAM (1983)

Alzatea (Fig. 11) probably consists of two species. It was considered as lythraceous by Lourteig (1965), and was included in the widely circumscribed Crypteroniaceae by van Beusekom-Osinga and van Beusekom (1975). However, Alzatea is unique in several features. According to A. Graham and S. Graham, on whom we base part of this information, the species of Alzatea in Costa Rica "is almost epiphytic in habit, growing upwards via other trees in the cloud forests with only slender stem connections to the ground." It remains to be proven whether this is the case also with A. verticillata in South America. Baas (1979) and van Vliet and Baas (1975, 1984) in their anatomical evaluation found that Alzatea has different, trilacunar nodes, which they consider to be an ancestral rather than a derived feature (Baas, pers. comm.). In Alzatea, also, the arrangement of vascular tissue in petiole and midrib of leaves is different from that in Lythraceae, having a different ray type and possessing branched foliar sclereids, which are unknown in Lythraceae. Like the Lythraceae, rudimentary stipules are present, however (Weberling, 1968). Pentamerous apetalous flowers in a branched panicle are rare in Lythraceae. Stamen, connective, and microsporangium features are also different from those in Lythraceae; whereas, the pollen grains (Muller, 1975) lack any of the specializations, e.g., pseudocolpi, found in many Lythraceae and in all Crypteroniaceae and Melastomataceae. Unspecialized, similar pollen grains occur in some lythraceous genera, however. The placentation in Alzatea is parietal, thus differs from that in most Lythraceae. (Ammannia microcarpa DC., with parietal placentation, is aberrant within its genus and in Lythraceae; it exhibits reduced features, and does not approach Alzatea.) Alzatea according to Tobe and Raven (1984a) has a bisporic, Allium-type, embryo sac; as in Rhynchocalyx (Rhynchocalycaceae), but unlike all other Myrtales, the micropyle of the ovules is formed by the inner integument alone and the archesporium is multicellular. Also, according to S. Graham (1984; Tobe & Raven, 1984a), the seed shape and seed coat do not resemble those in Lythraceae.

Thus, it would seem justified to place Alzatea in a separate family, Alzateaceae. The family is formally described by A. Graham and S. Graham (Graham, 1984).



FIGURE 10. Pteleopsis apetala Vollesen from Tanzania; Rodgers coll.—A. leafy branchlet.—B. flowering branchlet with male and female flowers in the same inflorescence.—C. inflorescence.—D. female flowers.—E. same, longitudinal section.—F. fruits. (Orig., del B. Johnsen.)



FIGURE 11. Alzatea verticillata Ruiz et Pav. (Alzateaceae), from Peru: A-H. Klug 3349; I-K. Woykowsksi 6196.-A. twig.-B. bud.-C. flower.-D. part of flower, interior.-E. interior of tepal.-F. disk.-G. stamen in different views.-H. transverse section of ovary.-I. fruit.-J. transverse section of fruit.-K. seed. (From Lourteig, 1965.)

PENAEACEAE GUILLEMIN (1828)

This is a fairly uniform family of ca. seven genera and 20 species restricted to the winter rainfall area of South Africa. The family consists of shrubs or shrublets with opposite, broad or narrow leaf blades, provided in their axils with small stipules dissected into rows of hair-like structures, which are usually glandular (but developed as relatively long hairs in Stylapterus barbatus A. Juss.; Dahlgren, 1967a). In this feature the family agrees with certain Lythraceae. The inflorescences vary between branched panicles and racemes, or may consist of a solitary terminal flower (Saltera). The flowers are consistently perigynous, 4-merous, apetalous, and haplostemonous, the four stamens alternating with the sepal lobes. The hypanthium is large and colored especially in Glischrocolla (Dahlgren, 1967b), Endonema (Fig. 12; Dahlgren, 1967c), and Saltera (Dahlgren, 1968), which are bird-pollinated. In Endonema, but not in the other genera, the stamens are inflexed in bud, in a way resembling that for Mouriri of Melastomataceae (Fig. 14C; see also Morley, 1953). The connective in all genera is massively carnose, and the introrse microsporangia sometimes, as in Penaea and Stylapterus, are only about half its length. The pollen grains are generally squarish or rectangular, 3-6-colporate, and always provided with pseudocolpi isomerous with the apertures. The four carpels form a 4-locular pistil with a narrow filiform to fairly stout style provided in Stylapterus and Penaea with four wings, in which case the stigmatic papillae are in commissural position between the apical lobes of the stylar wings, an indisputably derived condition. Whereas, in Endonema each locule has two lower pendulous and two upper ascending ovules, each locule in the other genera has only two ascending ovules. The embryo sac formation is peculiar, conforming to the 4-sporic, 16-nucleate Penaea-type (Stephens, 1909). The fruit is capsular.

Within Penaeaceae differentiation has taken place in two directions: (1) towards a large, rigid, and brightly colored hypanthium, in connection with ornithogamy, and (2) towards specializa-

tions of the style, with four prominent wings, and commissural stigmas in flowers of mediocre size and with yellowish (-purplish) color.

Penaeaceae show similarities to the Oliniaceae, Rhynchocalycaceae, Memecylaceae, Melastomataceae, and Lythraceae, most of which have perigynous flowers, minute stipular structures in axillary rows, pollen grains with pseudocolpi isomerous with the apertures, and prominently developed connectives.

The ancestors of Penaeaceae could have had common origin with Rhynchocalycaceae, in which the petals are somewhat reduced, the stamens alternate with the calyx lobes and are located on the rim of a receptacle, the connectives are well developed, the pollen grains are heterocolpate, the basic inflorescence type is paniculate, and the geographic distribution is close, though Rhynchocalycaceae are more subtropical in South Africa. There are several differences, however, e.g., the numerous ovules in the 2(-3)-carpellate pistil in Rhynchocalycaceae.

Penaeaceae are distinct enough to warrant separate familial status.

RHYNCHOCALYCACEAE JOHNSON & BRIGGS (1984)

This family consists of the genus *Rhyncho-calyx* Oliv., with the single species *R. lawso-nioides* Oliv., in the eastern parts of South Africa. *Rhynchocalyx* has previously been included in Lythraceae (Oliver, 1894; and several other authors) or Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975) but is obviously out of place in both families.

It is a tree (Strey & Leistner, 1968) with decussate, opposite, entire leaves and fairly large paniculate inflorescences (Fig. 13) with small hexamerous flowers. These have an open hypanthium, which, with its six calyx lobes, has a stellate appearance. Six small, white, hood-like, lobate and unguiculate petals rise from the hypanthial rim. Below and opposite each of the petals is inserted a stamen, incurved in bud (as in *Endonema* of Penaeaceae and Memecylaceae) and with a basifixed anther having a somewhat broadened connective (as in the families mentioned). The pollen grains are 3-colporate-het-

FIGURE 12. Endonema lateriflora (L. fil.) Gilg, an orthithogamous member of the South African family Penaeaceae: A-J. Stokoe 2148; K. Zeyher 17.—A. branch end with unifloral lateral inflorescences.—B. unifloral inflorescence ("flower").—C-E. leaves of lower, middle and upper pair in B.—F-H. stamen; adaxial, lateral, and abaxial view.—I. pistil.—J. capsule.—K. seed. (From Dahlgren, 1967c.)



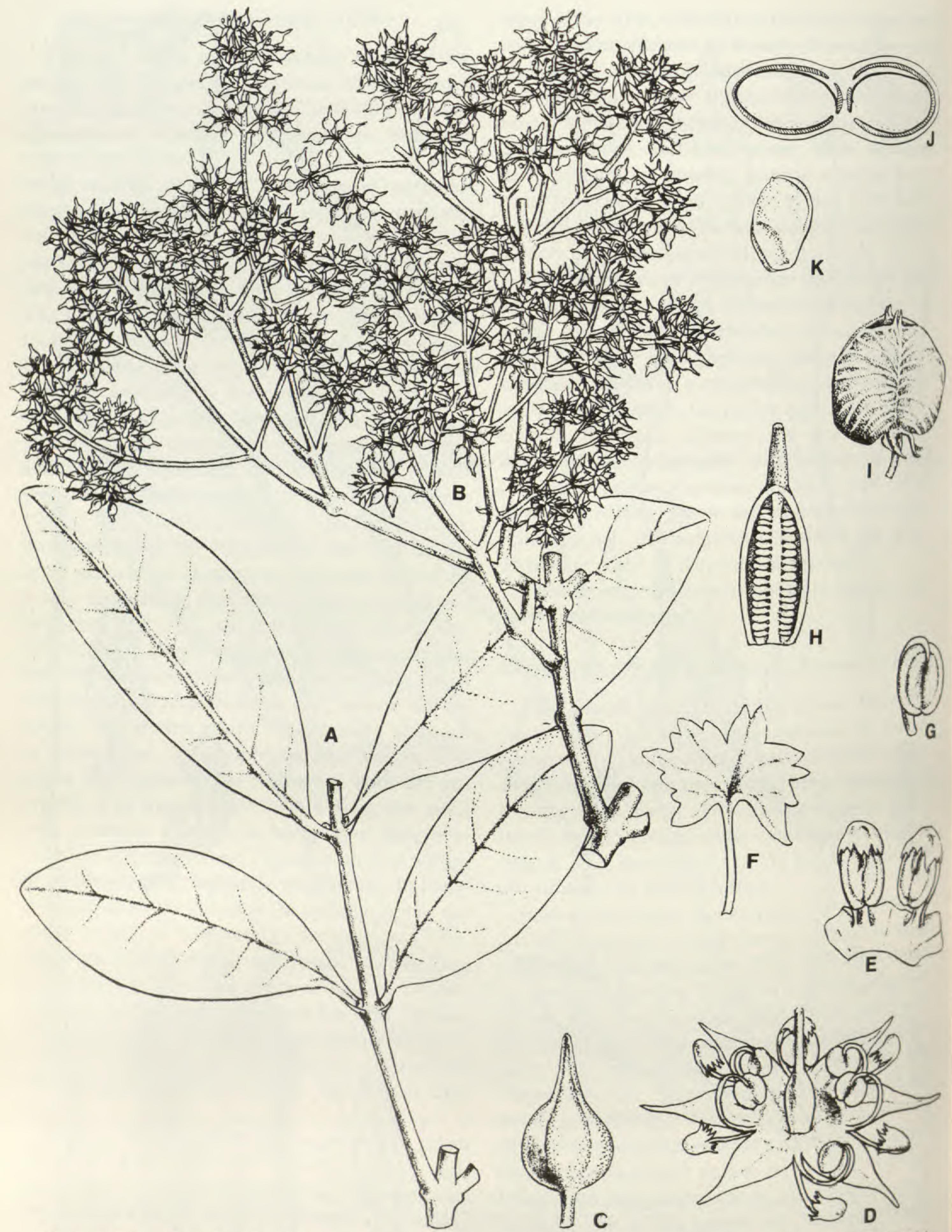


FIGURE 13. Rhynchocalyx lawsonioides Oliv. (Rhynchocalycaceae), from South Africa: A-H. Wood 3124; I-K. Strey 6539.—A. part of branch.—B. inflorescence.—C. flower bud.—D. flower.—E. two petals and two stamens on the hypanthial rim.—F. petal, flattened out.—G. stamen.—H. ovary in longitudinal section.—I. ripe fruit.—J. diagrammatic cross section of young fruit showing arrangement of seeds.—K. seed. (A-H from Oliver, 1894; I-K from Strey & Leistner, 1968.)

erocolpate, with three distinct pseudocolpi. The ovary is bi- (rarely tri-) carpellate and described by van Beusekom-Osinga and van Beusekom (1975) as unilocular, with two longitudinal placentae with numerous ovules, but it is partly bilocular. The style is simple and undivided. The fruit (Strey & Leistner, 1968) is a 2- (or 3-) locular capsule. It is cartilaginous, partly loculicidal, and contains 11–17 flat seeds per locule.

Unlike the Penaeaceae, Rhynchocalyx has the Polygonum-type embryo sac formation; it is peculiar in having a micropyle formed by the inner integument alone instead of both integuments; the nucellus, as in Lythraceae, has a multicelled archesporium, but there are several differences between Rhynchocalyx and Lythraceae that argue against a close relationship. (The embryological information according to Tobe & Raven, 1984b.) There are also embryological differences from Alzatea and Axinandra (Tobe & Raven, 1983b, 1984b), which support treating Rhynchocalyx as a family. The wood anatomy of Rhynchocalyx agrees well with that in Lythraceae, however (van Vliet & Baas, 1984). The chromosome number is n = 10 (Goldblatt, 1976), as is also the case in Penaeaceae, for example.

A comparison between Rhynchocalycaceae and other families is given by Tobe and Raven (1984b). The arguments for including the genus in Crypteroniaceae are weak, and it is also clear that the genus is best treated as distinct from the Lythraceae. A link with Penaeaceae (see under this family) is likely, but embryology does not support the inclusion of Rhynchocalyx in that family.

CRYPTERONIACEAE A. DE CANDOLLE (1868)

Crypteroniaceae (Crypteronia, Fig. 14; Dactylocladus, and Axinandra with perhaps a total of ten species; Shaw, 1973) are trees with opposite leaves, having a marked midrib and brochidodromous venation, the anastomoses of which are close to the leaf margin. Small stipules are present (note that such are seldom recorded for Melastomataceae). The inflorescences are profuse to poor racemules and the flowers small, often unisexual, 4–5-merous, and perigynous to epigynous, and may lack or have small petals, which in Axinandra are connate apically (and shed simultaneously as an umbrella). The stamens are alternisepalous and inserted on the

margin of the receptacle, inflexed in bud, and with a wide connective, which is conduplicate in *Axinandra*. The pollen grains are 2- or 3-colporate, with apertures alternating with pseudocolpi. The ovary is 2-6-locular and develops into a chartaceous or woody capsule.

The embryology has been studied in Axinandra (Tobe & Raven, 1983b). It differs from all other Myrtales known in having an endothelium (i.e., integumentary tapetum).

This family has recently been circumscribed and redefined by van Beusekom-Osinga and van Beusekom (1975), who, in addition to the three southeastern Asiatic genera, Crypteronia (Fig. 15), Dactylocladus, and Axinandra, which we here refer to the family, also included the Central and South American genus Alzatea and the South African genus Rhynchocalyx, each with one species only. The two last-mentioned genera, according to these authors, make up Crypteroniaceae subfam. Alzateoideae with paniculate inflorescences, superior bicarpellate ovaries, numerous ovules, and chartaceous capsular fruits. However, they do not seem closely allied to the former genera, nor to each other, and are best treated as separate families, Alzateaceae and Rhynchocalycaceae.

The Asiatic genera (van Beusekom-Osinga, 1977) may form a monophyletic group, although even this is somewhat uncertain. Among them, Axinandra was considered by Meijer (1972) as particularly primitive due to its 5-merous flowers with 10(-12) stamens. The caducous petals fall off as a cap when the flower opens (as in Eugenia), and the capsular fruit opens with five valves. In these features the genus was said by Meijer to approach various other families, such as Lythraceae, Memecylaceae, and the tribe Macarisieae of Rhizophoraceae.

Morley (1953) comments on the relationship between Axinandra and Dactylocladus (Crypteroniaceae) and the genera of our Memecylaceae and Melastomataceae. He finds that the two genera differ from the Memecylaceae in lacking included phloem in the secondary xylem, in lacking terminal sclereids and anther glands, and in having anatropous rather than campylotropous ovules, antesepalous ovary locules, different floral vascularization, and capsular fruit. Thus, these genera should not be included among the Memecylaceae, but would require a separate subfamily. We believe they can, provisionally,

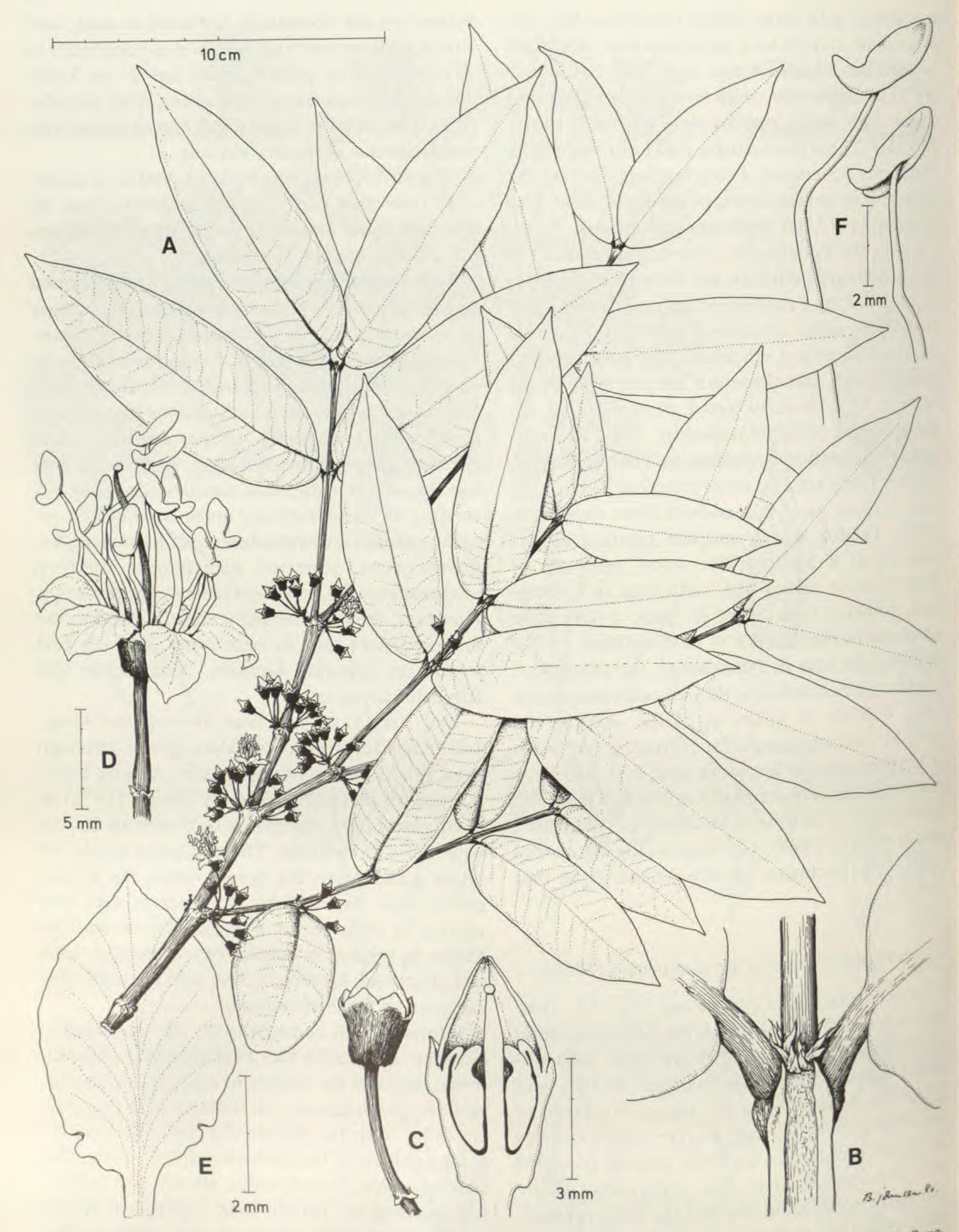


FIGURE 14. Crypteronia paniculata Kurz. (Crypteroniaceae), from collections made in Thailand: A-C. Sang-kachand et al. 1554; D. Larsen 8695.—A. branch with spikes of male flowers.—B. branch tip showing auricles of stem lists.—C. male flower.—D. female flower. (Orig., del. B. Johnsen.)

be treated with Crypteronia in the family Crypteroniaceae.

MEMECYLACEAE DE CANDOLLE (1828)

Although there are still doubts about the distinctness of this family, it is recognized here by one of us (Dahlgren) in accordance with the conclusions by Johnson and Briggs (1984), the alternative being to treat it as a subfamily under Melastomataceae (Thorne). It consists of 6–8 genera, the New World Mouriri (Fig. 15) and Votomita, and the Old World Lijndenia (Bremer, 1982), Memecylon, Spathandra, and Warneckea. The distinctness of Spathandra is still in dispute. Pternandra is discussed below.

They are mainly large shrubs to huge trees with opposite leaves having mostly pinnate venation with indistinct lateral and intramarginal veins. Stipules are probably generally absent; but Figure 15B shows a species of *Mouriri* with a row of finger-like structures (dissected stipules), which agree with the stipules in various other families of Myrtales, e.g., Penaeaceae.

Anatomically the family stands out as distinct (van Vliet, 1981; van Vliet et al., 1981; van Vliet & Baas, 1984) in having included phloem of the foraminate type (lacking in Melastomataceae), diffuse and mostly solitary vessels (frequently in multiples in Melastomataceae), the fibers have distinctly bordered pits (in Melastomataceae the fibers are libriform). Fiber dimorphism occurs in many Melastomataceae but not in Memecylaceae.

The indumentum is much less developed than in Melastomataceae. The richness and variation of foliar sclereids (incl. terminal sclereids) is conspicuous. Stomata have been found to be paracytic (Memecylon) or occur in crypts (Mouriri). The leaf tissues contain crystal druses (Baas, 1981).

The flowers are generally small and less differentiated than in most members of Melastomataceae. The stamens are twice as many as the petals and have a carnose, compact connective generally provided with a gland, and the anthers are longitudinally dehiscent. As in Melastomataceae, Crypteroniaceae, and Penaeaceae, the pollen grains are consistently heterocolpate. The ovary is inferior and contains 1–5 locules, each with two to numerous ovules. The embryology largely coincides with that for Melastomataceae, except that the seeds are different. The fruit is baccate with large or (Pternandra) rather small

seeds, generally with extensive, folded cotyledons (Bremer, 1981).

Morley (1953) defined this group by the presence of included phloem in the secondary xylem, pinnate leaf venation, occurrence of terminal sclereids on the vein endings in leaves and often in flowers, presence on the connectives of an elliptic or circular depressed gland, antepetalous ovary locules (when locules are isomerous with the petals), campylotropous ovules, relatively few and large seeds, and characteristic floral vascularization, all characteristics which do not apply to Pternandra, however. Morley (1953) considered the closest relatives of Memecylaceae sensu stricto to be the tribe Kibessieae, in which Pternandra (incl. Kibessia) has most of the memecylaceous features but leaf blades of the typical parallel, melastomataceous type. Pternandra also lacks terminal sclereids, it lacks a gland on the connective, and has numerous anatropous ovules and small seeds, but yet is probably best placed in Memecylaceae.

MELASTOMATACEAE A. L. DE JUSSIEU (1789)

The Melastomataceae consist of perhaps 195 genera and 3,500-4,000 species. These range from small, sometimes epiphytic herbs or shrublets to shrubs or, more rarely, lianas or trees. Nearly all have opposite leaves, which, characteristically, have 3-9(-19) main veins separate from the base of the blade. The leaves are entire in nearly all taxa, but have distinct, sometimes conspicuous teeth in Sonerila tenuifolia Bl., where the teeth seem to be an innovation and are different from those in Lythraceae and Onagraceae. Pellucid dots are generally absent, but occur in the genus Microlicia, where their presence and nature deserves attention. Stipules seem to be lacking. The nodes are unilacunar (van Vliet & Baas, 1984). Crystals occur as druses in all tribes except the Astronieae, where there are styloids instead; druses also occur in Memecylaceae and Crypteroniaceae where small styloids are also present (Baas, 1981). Interxylary (included) phloem appears to be lacking; libriform fibers are characteristic, and the fibers are often septate, these conditions representing differences from those in Memecylaceae (van Vliet & Baas, 1984). The stomata are generally anomocytic or polycytic (rarely diacytic, cyclocytic, or anisocytic), and the indumentum is extraordinarily differentiated, the trichomes being generally large, multi-



FIGURE 15. Mouriri chamissoniana Cogn., a Brazilian member of Memecylaceae; Hatschbach 20223.—A. branch.—B. bases of leaves showing axillary stipules as well as stem lists ending in "auricles."—C. floral bud, to the right in longitudinal section, showing inflexed filaments.—D. flower in full blossom.—E. petal.—F. stamens, note the difference in filament length within a flower. (Orig., del. B. Johnsen.)

cellular, and scale-like. The flowers vary in size from small and nearly actinomorphic to large, conspicuous, and distinctly zygomorphic, and are generally wholly or partly epigynous, the ovary generally densely beset with complex hairs. The petals, as in much of the order, are commonly pink to crimson or violet.

Stamens are in one or two whorls (diplo-, hap-lo-, and obhaplostemonous), with their filaments inflexed in bud and their connectives generally well developed, often prolonged or provided with appendages. The anthers are often poricidal but frequently open with longitudinal slits. The pollen grains as far as known (Patel et al., 1984; Carlo Hansen, pers. comm.) are consistently heterocolpate, being supplied with pseudocolpi or with intercolpate depressions isomerous with the usually three apertures.

The gynoecium is generally 3–5-carpellate, and the ovary 3–5-locular, only rarely unilocular where the partitions are dissolved, with axile or rarely basal placentation. The embryology is fairly typical of the order and shows no obvious specializations. The fruit is baccate or capsular with seeds smaller than in most genera of Memecylaceae. Its embryo also has smaller and less folded cotyledons, which may be equal or unequal (cf. Trapaceae). The seed coat lacks fibers in the exotegmen.

With this circumscription Melastomataceae becomes a rather homogeneous family. The genus *Pternandra* of Memecylaceae at least phenetically shows some features of Melastomataceae; some of these may be plesiomorphies (lack of connective gland, lack of terminal sclereids, small seeds), others convergences (leaf venation). It may be regarded as intermediate, which is an argument for including Memecylaceae as a subfamily in Melastomataceae, as preferred by one of us (Thorne).

PSILOXYLACEAE CROIZAT (1961)

This family is closely allied to Myrtaceae and, using a broad family concept, may well be included in that family (Schmid, 1980). It is monotypic, consisting of the genus *Psiloxylon* with the species *P. mauritianum* (Hook. f.) Baill. on the Mascarene Islands. The genus is a small tree with pseudo-alternate (disjunct-opposite), stipulate, glabrous, and gland-dotted leaves and small, axillary panicles. Divided myrtalean stipules are present at least in young plants (Johnson & Briggs,

pers. comm.). The flowers are unisexual, 5(-6)merous, and perigynous, with a nectariferous floral tube, free sepals and petals, and diplostemonous androecium. In the female and male flowers the stamen-like staminodia and a pistillike pistillode, respectively, are present. The stamens are erect in bud, a rare feature in Myrtaceae, but the pollen grains are conspicuously similar to those in Myrtaceae. The tri- (bi-, quadri-) carpellate pistil is clearly superior and often has a (very) short stipe; it has an extremely short style and the (2-)3(-4) stigma-lobes are flat and reflexed. In these characteristics Psiloxylon differs from nearly all Myrtaceae. The ovary is trilocular and has axillary placentas, each with numerous anatropous ovules. The fruit is a berry. (Information mainly from Schmid, 1980.)

In anatomical respects (van Vliet & Baas, 1984), Psiloxylon shows a distinctive combination of features and has, for example, chambered, crystalliferous fibers, lacking in the Myrtaceae. Psiloxylon also has a cancellate testa, which is very rare in Myrtaceae.

In the light of a number of distinctive features it seems justifiable to treat *Psiloxylon* as a distinct family rather than as a member of Myrtaceae as treated by Schmid (1980). The presence of secretory cavities and sunken styles, and the pollen morphology are shared with the following two families and support the common evolution of Psiloxylaceae from the same ancestors as Myrtaceae and Heteropyxidaceae. With a broader family concept the three families could be treated as one (as preferred by Thorne).

HETEROPYXIDACEAE ENGLER & GILG (1919)

It is with doubt that this family is acknowledged here, by one of us (Dahlgren), in accordance with Johnson and Briggs (1984), the alternative being to include it in Myrtaceae either as a subfamily (as preferred by Thorne) or without discrimination at all (Schmid, 1980).

The single genus Heteropyxis, with three species in southeastern Africa, consists of shrubs or small trees with disjunct-opposite ("alternate"), entire leaves with minute stipules. The leaves, as in Myrtaceae and Psiloxylaceae, are gland-dotted. The anatomy seems to agree with that in Myrtaceae, although the cork is not stratified, as is usually the case in Myrtaceae; vasicentric tracheids are lacking (usually present in Myrtaceae) and axial parenchyma is lacking (rare in Myrtaceae)

tales) (data from Schmid, 1980). In some of these features Heteropyxidaceae agree with Psiloxylaceae. The inflorescence is a small panicle of unisexual, actinomorphic, perigynous, tetramerous or pentamerous flowers. Sepals and petals are imbricate and free, and the androecium, usually of (5-)8 stamens, are obdiplostemonous or rarely obhaplostemonous. The stamens are erect in bud, the anthers longitudinally dehiscent, and the pollen grains are triangular and syncolporate, similar to those in Myrtaceae, lacking pseudocolpi. The pistil is generally bicarpellate, with sunken style, much longer than in Psiloxylaceae, and with capitate stigma. The fruit is a dry loculicidal capsule with persistent style. The embryological information available is in accordance with the Myrtaceae.

Similarities between Heteropyxidaceae and Psiloxylaceae are the spiral phyllotaxy, the stamens that are erect in bud stage, and the reduced carpel number. Both are primitive in having perigynous flowers. On the other hand, Heteropyxidaceae differ from Psiloxylaceae as well as Myrtaceae in a number of respects (see Johnson & Briggs, 1984).

MYRTACEAE A. L. DE JUSSIEU (1789)

This is a large family of ca. 145 genera and more than 3,650 species (Schmid, 1980) with wide, chiefly tropical-subtropical distribution and a center in Australia, but also with many taxa in South America. As this family will be dealt with in more detail by other participants of this symposium, only a few remarks will be made here. Myrtaceae have generally been divided into two subfamilies, Myrtoideae and Leptospermoideae. Schmid (1980) reviewed the subfamilial history of the family and recognized two additional subfamilies: Chamaelaucioideae (formerly a tribe in Leptospermoideae) and Psiloxyloideae. For various reasons and in line with Johnson and Briggs' treatment of Myrtaceae (1984), we have excluded Psiloxylon and Heteropyxis as separate families (or subfamilies, Thorne), and abandoned the traditional division of Myrtaceae into (other) subfamilies.

The family is a fairly distinct one, characterized in particular by having gland-dotted leaves, stems, and floral parts (as do Psiloxylaceae and Heteropyxidaceae). In the presence of schizolysigneous secretory cavities filled with essential oils (monoterpenes, sesquiterpenes, phloroglucin derivatives of baeckerol, eugenin, and tasmonol

types, etc.) Myrtaceae, Heteropyxidaceae, and Psiloxylaceae are distinctive in the order. The calyx and corolla are imbricate and the stamens are usually numerous, although very occasionally few. The inflorescences are basically paniculate. The evolutionary trends within Myrtaceae are presented in detail by Briggs and Johnson (1979). The flowers are nearly always epigynous and bisexual, nearly always actinomorphic, 4-or 5-merous (other merous conditions are not rare), with a floral tube of variable length often prolonged above the ovary, on the margin of which the sepals, petals, and normally numerous stamens are all inserted. The sepals or petals or both are occasionally fused, either into a cap (or operculum) that is shed at anthesis, or else the fused perianth ruptures irregularly. The androecium is usually polystemonous, very occasionally paucistaminal and then obdiplostemonous, diplostemonous, obhaplostemonous, or haplostemonous. When the stamens are numerous they may be evenly distributed or very occasionally appear in (basically five) fascicles (nearly always antepetalous); the fascicled condition is reminiscent of that in Hypericaceae, with the fascicles nearly always opposite the petals. The developmental succession of the polystemonous androecium is, however, centripetal. The connectives are only rarely enlarged although they usually have one or more apical secretory cavities (glands). The anthers dehisce by slits or (for example in certain sections of Eucalyptus and in the Chamaelaucium-group) by pores. The pollen grains are generally triangular, often syncolp(or)ate, and lack pseudocolpi. Staminodia are rarely present. There is great variation in number of loculi (carpels) of the pistil, which range from one to 16 per flower, three, four, five, and especially two being predominant (Schmid, 1980, tables 3, 4). The placentation is usually axile, occasionally subbasal, basal, or apical; the number of ovules per ovary is usually numerous, occasionally few, very rarely one. One feature of note is that the ovules are usually described as lacking a parietal cell. Davis (1966), however, suspects that the parietal cell is cut off so early that it has escaped notice, because parietal tissue is formed without periclinal divisions in the nucellar epidermis (except in P_{SI} dium).

The fruit is fleshy or dry, respectively a berry or loculicidal (very rarely circumscissile) capsule, very occasionally a drupe, schizocarp, or indehiscent, nutlike structure, and there is great variation in the shape of the embryo. Both fruit and

embryo are useful in the division of the family. Each fruit usually contains one to few, though very occasionally many, fertile seeds. The endosperm is initially nuclear and is usually lost at seed maturity, occasionally a scant amount of endosperm being present. The embryo sometimes contains copious amounts of starch.

Except for Psiloxylaceae and Heteropyxidaceae, which Schmid (1980) included in Myrtaceae, the family shows no obvious connections with the other families of the order. *Punica*, in its polymerous androecium, lack of pseudocolpi, etc., is reminiscent of Myrtaceae (convergence), but the relationship is probably not close. A phylogenetic link with Lecythidaceae has been proposed but is not supported by detailed examination.

INTERRELATIONSHIPS OF FAMILIES AND EVOLUTION WITHIN MYRTALES

To approach the interrelations between families in Myrtales it may be profitable to deduce a probable original state for their common ancestors. This can best be done by comparing the character states of the myrtalean families interse and by examining those of probably related orders, Rosales being chosen as the outgroup.

The myrtalean ancestors were probably woody plants with alternate or opposite leaves, the margins of which possibly had lateral teeth with a hollow, crater-like apex. Stipules were presumably present but minute, entire, and situated laterally. The stem had evolved bicollateral vascular strands and the vessel elements had alternate, vestured pits and end plates with entire perforation or scalariform perforation with few bars. Furthermore, the ground tissue of the wood consisted of fiber-tracheids, the wood parenchyma was paratracheal and apotracheally diffuse, and the rays were heterogenous (van Vliet & Baas, 1984). Crystals most likely occurred in the axial parenchyma and in the ray cells. The stomata probably were anomocytic, and no complicated trichomes were developed. The flowers, in determinate, paniculate inflorescences, were actinomorphic, perigynous, and diplostemonous, 5- or 4-merous, and petaliferous. The pistil was eusyncarpous with axile placentation, a simple style, and a lobate or branched stigma. The stamens did not have a particularly swollen or Otherwise differentiated connective. The anthers dehisced longitudinally, the tapetum was glandular, and the pollen grains were binucleate at

anthesis and most likely 3-colporate, lacking pseudocolpi; viscin threads were lacking. The ovules were anatropous, bitegmic, and crassinucellate with a parietal cell cut off from the archesporial cell in the nucellus. The embryo sac formation proceeded according to the *Polygonum*-type, endosperm formation was nuclear, and the ripe seeds had a very thin endosperm and a well-developed embryo probably containing protein and fat. The fruit was presumably capsular. In the seed coat, the exotegmen was probably not fibrous, and the mesotestal layer probably did not contain sclerotic cells.

The immediately ancestral forms were tannin plants with a flavonoid spectrum based on flavonois of the commoner types. Ellagic acid and ellagi-tannins were synthesized. Triterpenes likewise were presumably present, whereas triterpene saponins may or may not have occurred.

None of the extant families exhibits this combination of attributes, though the family approaching most closely the ancestral form of Myrtales would have been fairly similar to certain extant Lythraceae. In this family the leaves may have teeth of the kind mentioned above, although they are "cryptic," and the leaf margin can be ciliate. Pellucid dots with essential oils are lacking. The flowers are also generally perigynous and generally petaliferous, diplostemonous, and perfect; the pistil is basically eusyncarpous; and the embryology agrees closely with the general, unspecialized pattern in the order, with, for example, the *Polygonum*-type embryo sac formation.

However, in Lythraceae, the wood does not have fiber-tracheids but libriform fibers, which are generally septate. The stipules quite often are specialized and dissected, forming one or two groups of hair-like structures located in the leaf axils (Fig. 8c). The stamens are generally free from the hypanthial tube and inserted inside this. generally at or near its base. This condition is dubiously primitive in the order, and may be derived from the general condition where the stamens, like the petals, are inserted on the rim of the hypanthial tube. Furthermore, the pollen grains in at least nine of the 25 genera are heterocolpate, the heterocolpate condition being probably ancestral in the family but derived within the order. Finally, the seed coat with its fibrous exotegmen represents a specialized type.

Therefore, the Lythraceae should be excluded from consideration as wholly unspecialized. However, their position in the order is central,

and they show close relationship with several of the families, including Penaeaceae, Rhynchocalycaceae, and Onagraceae.

A number of the supposedly primitive states are concentrated, perhaps to a higher degree than in Lythraceae, in Psiloxylaceae, Heteropyxidaceae, Myrtaceae, and Strephonematoideae, although each of the taxa is specialized in various respects. The varied rates of evolutionary specialization throughout the order are illustrated by *Psiloxylon*, which has retained the presumably ancestral condition of diplostemonous flowers with a wholly superior ovary but has libriform and septate fibers, which are presumably derived. Most Myrtaceae have numerous stamens and a more or less inferior ovary, but their wood is generally characterized by having fibertracheids.

We have refrained from giving a cladistic presentation of the probable evolution in Myrtales, as this is done elsewhere in this volume, by Johnson and Briggs (1984), on the basis of the same data. However, we find it appropriate to discuss the probable or at least possible evolutionary courses that might have taken place in the order, as our opinions may deviate in certain major as well as minor features from those of other authors.

An evolutionary line that probably diverged very early from the myrtalean ancestors is represented by Psiloxylaceae, Heteropyxidaceae, and Myrtaceae. These share some conspicuous features, such as the characteristic shape and aperture conditions (syncolpate) of the pollen grains (Schmid, 1980; Patel et al., 1984) and the presence of schizolysigenous cavities with essential oils visible as pellucid dots on the green parts. The first representative of this evolutionary line doubtless had diplostemonous flowers with superior ovary such as in present day Psiloxylaceae, but the latter are specialized in having, for example, unisexual flowers with an extremely short style and reflexed, flat and carnose stigma lobes. The great concordance in pollen morphology among Psiloxylaceae, Heteropyxidaceae, and many Myrtaceae indicates that this rather peculiar type evolved very early from proto-myrtaceous ancestors and later in many Myrtaceae gave rise to superficially simpler kinds. The fact that this kind of pollen is known already in the Cretaceous (ca. 72 million years ago), before any other certain Myrtales, also indicates that this group of families was differentiated from the myrtalean ancestors very early.

Also Onagraceae seem to deviate rather strongly from other Myrtales, and probably evolved as a lateral evolutionary line at an early stage. The evidence is somewhat contradictory in this respect. The family is an unusually distinct one in having the combination of epigynous flowers, pollen with viscin threads, *Oenothera*-type embryo sac formation, and tissues with calcium oxalate raphides. The latter three characteristics are absent from nearly all other Myrtales, and it is likely that all these character states are derived ones.

Thus, it is unlikely that other families, such as the Trapaceae, could have evolved from the onagraceous evolutionary line after these attributes had been acquired. In pollen-grain shape and pollen-wall structure Onagraceae show some general similarity to Myrtaceae, Heteropyxidaceae, and Psiloxylaceae (Nowicke, pers. comm.). But more conspicuous are a number of characteristics shared by Onagraceae and Lythraceae: wood with libriform and septate fibers; leaves with lateral teeth that have the same hollow and crater-like apex ("Fuchsioid" subtype, Hickey, pers. comm.), petals with similar, pinnate venation (Chrtek, 1969); and seed coat with fibrous exotegmen (Corner, 1976). With the probable exception of the leaf teeth, these attributes seem to represent derived states, and should be so considered. Convergent evolution of some of the derived states is not unlikely; though more likely is the alternative that Onagraceae diverged from proto-lythraceous ancestors after the wood and seed-coat structures had already evolved.

A probable appearance of epigyny in two independent lines of evolution in the onagraceous ancestors has been proposed by Eyde (1981) on the basis of the position of the nectaries on opposite sides of the ovary/hypanthium junction. In this feature the genus *Ludwigia* differs from all other Onagraceae.

The remaining families of the Myrtales form a somewhat coherent group, most families being characterized by so-called "heterocolpate" pollen grains, in which pseudocolpi are present between the true apertures. This feature is extremely rare in angiosperms outside the Myrtales, and it would be highly unlikely that pseudocolpi evolved independently in several phyletic lines within the order. Accordingly, we presume that the genetic constitution for pseudocolpi (whether expressed or not) evolved once in the common ancestors of these families, but that it may have "become lost," i.e., the attribute has not come

to expression, in some lines. Thus, for example, in Lythraceae pseudocolpi occur in some but not in all genera (see above and in Patel et al., 1984); in some genera they are indistinct or inconsistently present. In Lythraceae at least *Lythrum* has pseudocolpi of the same number as the true apertures whereas in most lythraceous genera with pseudocolpi these are twice as many as the apertures.

Pseudocolpi are absent (or very indistinct) in the pollen grains of Alzateaceae and Lythraceae subfam. Punicoideae, Sonneratioideae, and Duabangoideae, in Combretaceae subfam. Strephonematoideae, and in Trapaceae, where the intercolpate depressions dubiously correspond to pseudocolpi. The first five taxa, which are all few in species, show strong affinity, as expressed by similarities in various respects, to families or subfamilies where the pollen grains possess pseudocolpi, and thus it is likely that their common ancestors had heterocolpate pollen grains.

Among the families where heterocolpate pollen grains are prevalent, some are characterized by having a seed coat with fibrous exotegmen and some lack fibers in this layer. A fibrous exotegmen was claimed by Corner (1976) to have great phylogenetic significance, and he suggested that this could serve as the basis for distinguishing a number of families from Myrtales sensu stricto as the order Lythrales. Although it is now obvious that this division would be unnatural, the fibrous exotegmen cannot be entirely ignored at the suprafamilial level.

A fibrous exotegmen occurs in Lythraceae with all its subfamilies, in Trapaceae, and Combretaceae (Oliniaceae remain to be investigated). Wood-anatomical, embryological, and other attributes strongly support close relationship between the subfamilies of Lythraceae, previously treated as several families, indicating thus considerable value for this seed coat attribute.

Trapaceae are often associated with Lythraceae (cf. Miki, 1959, who derives Trapa from Lythrum through Hemitrapa; but see also Vasil'ev, 1967, who disagrees with Miki). The family is unique in the order in many respects, however, as a specialized floating aquatic, the decussate leaves of which form a rosette. The leaf blades are provided with lateral teeth which deviate from those of other Myrtales in having a unique double apex (Hickey, 1981). The tetramerous, haplostemonous flowers are nearly perigynous; the fruit is dry, indehiscent, and provided with characteristic horns; the endosperm formation is ar-

rested in the initial stage (as in orchids); one of the cotyledons is reduced; and the embryo is filled with starch. In these features *Trapa* has diverged strongly from other Myrtales and from any plausible ancestral type. The pollen morphology of Trapaceae may indicate affinity with the heterocolpate condition if the intercolpate areas between the meridional crests are homologous to intercolpate depressions and, hence, to pseudocolpi, but this is far from settled. (Intercolpate depressions substitute for pseudocolpi, for example, in various Melastomataceae.)

There is some variation within Lythraceae in the possession of sclereids. Thus, these are present in subfam. Sonneratioideae and Duabangoideae, whereas only few Lythroideae have unbranched sclereids restricted to the leaf petioles. The first two subfamilies also deviate from nearly all Lythroideae in having the stamens inserted on the rim of the hypanthial tube. Both these traits may be ancestral in the lythraceous line of evolution. In nearly all taxa of Lythroideae, the stamens are inserted inside the hypanthial tube or near its bottom and in subfam. Punicoideae the numerous stamens are inserted on the upper, inner part of the hypanthium. The flowers are generally diplostemonous in subfam. Lythroideae, but in certain genera (see p. 649) are haploor obhaplostemonous. In the relatively large flowers of subfam. Sonneratioideae, Duabangoideae, and Punicoideae, the stamens are numerous.

The different sequence of initiation of the androecium (centripetal in subfam. Sonneratioideae and Duabangoideae and centrifugal in subfam. Punicoideae and certain genera of subfam. Lythroideae) suggests that the multistaminate condition has evolved along several different lines in Lythraceae. Similarly, the haplo- and obhaplostemonous condition has certainly evolved along several separate lines in the family.

Within subfam. Lythroideae the polymerous, large-flowered genera, such as Lafoënsia and Lagerstroemia have numerous stamens (in the former only diplostemony, however) and unspecialized pollen grains, lacking pseudocolpi. In these features they are generally considered to be primitive, a view that we wish to challenge. More likely, an increase in floral size has involved increase in number of sepals, petals, and carpels and especially has favored an increase in stamen number. Lack of pseudocolpi is found in about half of the lythraceous genera studied, and does

not seem to characterize natural groups of genera in subfam. Lythroideae (Graham & Graham, pers. comm.). The reasons for considering absence of pseudocolpi as derived in the family are mentioned elsewhere in this article. In contrast to all other myrtalean families the pseudocolpi, when present, tend to be double the aperture number, a condition which should be considered another derived character state.

How the first differentiation proceeded in the common ancestors of Lythraceae is perhaps impossible to deduce. As the insertion of stamens on the hypanthial rim is the normal state outside Lythraceae (some Combretaceae excepted), we presume that this was the ancestral state, and that their insertion inside the hypanthium is an apomorphy that arose in the ancestor of subfam. Lythroideae and, perhaps, Punicoideae. Punicoideae should have differentiated early from the latter line with its epigyny, increase in stamen number, indehiscence of fruit, acquisition of sarcotesta, etc. Alternatively, epigyny could have arisen in a common ancestor of the three small, unigeneric subfamilies. The discrepancy in anatomical details, in fruit, chromosome number, etc. suggest that Duabanga and Sonneratia differentiated early from each other, Sonneratia having possibly arisen at a later stage from the common lythraceous line.

A fibrous exotegmen is also found in the seeds of Combretaceae and, although not known in Strephonema, it is likely that it is the case in this genus, too. A considerable number of features are common to the subfamilies Combretoideae and Strephonematoideae, among them the combretaceous hair type (Stace, 1965), the racemose inflorescence type, obdiplostemony, at least some degree of epigyny (only partial in Strephonematoideae), and the unilocular ovary. Strephonema differs from other Combretaceae in the only hemi-epigynous flowers, in stomatal type and in several wood-anatomical features (van Vliet & Baas, 1984), which may justify separation at family level (see Venkateswarlu & Prakasa Rao, 1971), but as they are so obviously related, subfamily rank may be sufficient.

Oliniaceae agree with Combretaceae in several features, e.g., epigyny and the frequent occurrence of small petal scales, and also share the basic chromosome number (X = 12) and the geographical distribution, centered in Africa, but seem to belong rather to the following branch.

A number of families, mostly with heterocolpate pollen grains, have seeds without a fibrous exotegmen but often with sclerotic cells in the mesotestal layer. Although Oliniaceae are unknown in the latter respect, they probably belong in this group as is indicated by the number of features shared with Penaeaceae and Rhynchocalycaceae. These families are Melastomataceae, Memecylaceae, Crypteroniaceae, Rhynchocalycaceae, Penaeaceae, and Alzateaceae. Alzateaceae (Alzatea) probably belong to this group, although their pollen grains lack pseudocolpi. In all these families the leaves have a fixed, opposite phyllotaxy, and the stamens are inserted on the hypanthial rim, both features of which may, however, be ancestral (plesiomorphies). The connective is also frequently enlarged in these families.

The two unigeneric families Alzateaceae and Rhynchocalycaceae share a number of wood-anatomical characters (van Vliet & Baas, 1984), which makes it likely that they are closely allied, and in which they differ from especially Penaeaceae, which they otherwise resemble in floral characters. It is extraordinarily difficult to reveal whether wood-anatomical features have evolved by convergence here. Fiber-tracheids, which are considered primitive, are found in Penaeaceae, Memecylaceae, and Crypteroniaceae, whereas libriform and septate fibers have arisen in Melastomataceae and, probably independently, in Oliniaceae, Rhynchocalycaceae, and Alzateaceae; the last three families perhaps being rather closely allied.

Whereas Memecylaceae have fiber-tracheids and solitary vessels, they are derived in having included phloem and also epigynous flowers, and, as a rule, large seeds with curved embryos. The Crypteroniaceae, here restricted to the three Asiatic genera Crypteronia, Dactylocladus, and Axinandra, are a variable group which also has retained primitive wood features but adopted diverse specializations in the flowers of each genus. Whether all three genera have an integumentary tapetum, as in Axinandra (Tobe & Raven, 1983b), is uncertain. Parallel are the Melastomatoideae which are specialized both in the wood with libriform and septate fibers and aggregated vessels, in their more developed indumentum, and in their leaf venation.

It is conspicuous that the mentioned three families show very few synapomorphies, and thus may not be so intimately interrelated as has generally been presumed.

Penaeaceae, which have also retained a primitive wood anatomy, approaches the mentioned families, but are also closely connected with Oliniaceae, Rhynchocalycaceae, and Alzateaceae in

various floral characters, e.g., in the obhaplostemonous condition. The bisporic Allium-type embryo sac in Alzateaceae (Alzatea) (Tobe & Raven, 1984a) may or may not be seen as a step in the direction toward the tetrasporic Penaeatype of Penaeaceae; at least the deviation from the Polygonum-type may have a common genetic basis. Both families have apetalous, perigynous flowers with prominent connectives. Alzateaceae are, however, very isolated by having trilacunar nodes and a different arrangement of vascular tissue in petiole and midrib of leaves (van Vliet & Baas, 1984), pollen grains lacking pseudocolpi (Muller, 1975), which we consider a derived state in this case, and a bicarpellate unilocular ovary with parietal placentation. In all this it appears as a distinct and isolated taxon, and the close connection with Rhynchocalyx indicated by the bicarpellary ovary and other details that caused the treatment of these genera in a subfamily of Crypteroniaceae, earlier, may largely be due to convergence.

Penaeaceae, Rhynchocalycaceae, and Oliniaceae, all with African distribution, may be closely interrelated, the last two more advanced in wood anatomy. Penaeaceae and Rhynchocalycaceae in particular resemble each other in the basically complex paniculate inflorescences, the obhaplostemonous flowers, the conspicuous connectives of the anthers, the heterocolpate pollen grains, and the basic chromosome number (X = 10), but the differences in wood anatomy, carpel and seed number, etc., still indicate some distance.

Oliniaceae and Penaeaceae each have a number of characteristic features (autapomorphies) but the two have rather few of their own synapomorphies.

We consider it very difficult to speculate about the interrelationships and evolutionary sequences for the Melastomataceae-Memecylaceae-Crypteroniaceae-Penaeaceae-Oliniaceae-Rhynchocalycaceae-Alzateaceae group, and refer to alternative interpretations presented by Johnson and Briggs (1984). Small differences in interpretation and small deviations from the most parsimonious evolutionary courses in this part may strongly change their evolutionary model.

FAMILIES ALLEDGEDLY RELATED TO OR IN VARIOUS RESPECTS CONSPICUOUSLY SIMILAR TO MYRTALES

Certain families have traditionally been linked with Myrtales, viz., Haloragaceae, Rhizophoraceae, Lecythidaceae, Thymelaeaceae, and, less

often, Elaeagnaceae. In addition to these, there are a few families which have a combination of attributes similar enough to those of myrtalean families that they also deserve mention here. These include Elatinaceae, Coridaceae, and Chrysobalanaceae.

THYMELAEACEAE

Thymelaeaceae, with perhaps 500 species in 50 genera (Shaw, 1973; Cronquist, 1981), are sometimes included in Myrtales (and are still so placed by Cronquist, 1968, 1981, 1984), and the family indeed possesses a number of myrtalean attributes. Some of these are evaluated here.

The family consists mainly of shrubs (rarely trees, lianas, or herbs). Most, but not all genera (not the Gonystyloideae), agree with the myrtalean families in possessing intraxylary (and often interxylary) phloem, vestured pits, and presence of elongate crystals in the wood (van Vliet & Baas, 1984). The phloem is permeated by a network of tough fibers. The leaves are alternate, opposite, or verticillate, entire, and have mucilaginous epidermal cells. They lack stipules, representing a difference from most Myrtales. The flowers are frequently 4-merous and perigynous with sepals, petals, and two whorls of stamens (diplostemonous) located on a more or less welldeveloped, frequently cylindrical or campanulate and brightly colored hypanthium. The petals are generally lacking or are small or reduced to entire or 2-cleft scales (cf. Oliniaceae). The pollen grains are pantoporate and crotonoid, reticulate or rarely with no sculptural pattern and are wholly unlike those in the myrtalean families, without connection with wind pollination, and are dispersed in the trinucleate stage, which is rarely the case in Myrtales. The pistil consists of two or rarely up to 12 carpels and may have as many locules, but it is generally unilocular, with a single, often excentric style (considered pseudomonomerous), a condition not met with in Myrtales, where the most nearly similar condition is that found in Combretaceae. Thymelaeaceae, like a few Combretaceae, also have an obturator descending from the base of the stylar canal to the ovules, and, as in the latter family, the ovules are pendulous. The embryological features differ to a considerable degree from the basic pattern in Myrtales (Tobe & Raven, 1983a). The fruit in Thymelaeaceae is generally indehiscent, rarely a loculicidal capsule. As in Myrtales, the seed generally possesses little endosperm; its embryo is rich in fatty oils and, as in some Myrtales (e.g.,

in Melastomataceae), has expanded, flat cotyle-dons.

Whereas some of these attributes might indicate a position in Myrtales, the embryological and chemical evidence strongly argues against this. Among the chemical features of Thymelaeaceae that may be mentioned are a lack of tannins, lack of ellagic acid, a different flavonoid spectrum (cyanidin, pelargonidin, delphinidin, methylated anthocyanidins, and myricetin all lacking), and presence of coumarins like daphnin and daphnetin. The lack of bicollateral vascular strands in the relatively primitive Gonystyloideae indicates that the thymelaeaceous ancestors did not have internal phloem. A number of taxonomists believe that Thymelaeaceae approach most closely Euphorbiales and Malvales, although further evidence for this affinity would be desirable. The very distinctive pollen of Thymelaeaceae is totally distinct from that of any Myrtales and similar to that of most Euphorbiaceae. There is also similarity between Thymelaeaceae and Euphorbiaceae in seed wall structure (Corner, 1976), in which Thymelaeaceae differ from the myrtalean families. Both authors consider that Thymelaeaceae should be placed near Euphorbiaceae, and that these two families are related to Malvales.

It seems important, in this context, to reconsider the homogeneity of Thymelaeaceae. Some evidence suggests that the Gonystyloideae are out of place in this family, and may, moreover, not even be closely allied to it. If this is supported by further evidence, then some of the arguments, but by no means the most important ones, against an affinity with Myrtales are removed. Yet, chemical, embryological, pollen-morphological, and other evidence still argues strongly against placement of Thymelaeaceae in this order. On the basis of pollen, Gonystyloideae do resemble other Thymelaeaceae closely in their unique exine, and the family is probably natural (Nowicke, pers. comm.).

HALORAGACEAE

This family has often been placed in Myrtales by virtue of its often opposite leaves with minute stipules, its 4-merous, basically diplostemonous flowers with four carpels, its similar embryology, and its exendospermous seeds. The family has recently been studied in detail by Orchard (1975, and various other papers).

Many vegetative features are in accordance

and vestured pitting are absent. According to Hickey and Wolfe (1975), who assigned Haloragaceae to Hippuridales, the leaf teeth are of the Rosoid type (similar teeth occur in some Onagraceae and Lythraceae; Hickey, 1981). Stipules (see above) are present and of a vestigial kind, as in Myrtales. Inflorescence characteristics provide little assistance in assigning Haloragaceae to any major complex. The floral anatomy of Haloragaceae (Orchard, 1975) shows similarity to that in Cornales and Araliales rather than to that in myrtalean families. Pollen morphology shows features connected with wind pollination, and comparisons with other groups (Orchard, 1975) give no clear indications of phylogenetic affinity. The pollen grains are shed in the tricellular stage as in Araliales, but unlike Myrtales. The gynoecium lacks a single style, and the stylodial parts are either very short, or there are separate stylodial branches, as in Araliales. The fact that the anther wall formation in certain taxa of Haloragaceae is of the monocotyledonous type may not be very informative because the dicotyledonous type also occurs in the family. More interesting, perhaps, is the fact that the endosperm formation in Haloragis and some species of Myriophyllum is of the possibly more basic cellular type, which is not known to occur at all in Myrtales. Embryo-sac formation is of the Polygonum-type, excluding any origin from within Onagraceae, and the embryogeny is of the Myriophyllum variant of the Caryophyllad type, in which the family differs from all Myrtales (Kapil, 1962; Kapil & Bala-Bawa, 1968). The seeds are often fairly rich in endosperm, which is not so in Myrtales; but in Araliales the endosperm is even more copious and the embryo proportionally smaller than in Haloragaceae.

with those in Myrtales; however, internal phloem

Our conclusion is that Haloragaceae seem to comprise a fairly isolated family. They possess a number of myrtalean attributes but these are counterbalanced by several dissimilarities. One of us (Dahlgren) cannot support Orchard (1975) in his conclusion that Haloragaceae has its closest connection with Cornaceae, because the unitegmic, tenuinucellate ovules, lack of tannins common presence of iridoids, and other details in Cornales (see below, p. 695) seem incompatible with the above-mentioned features of Haloragaceae. Orchard also found Haloragaceae to be similar in various respects to Rhizophoraceae and Combretaceae, the latter of which is clearly myrtalean. Thus Haloragaceae may better be

treated in an order separate from, but near Myrtales. In accordance with Orchard's findings, Haloragaceae should be separated from Gunneraceae and Hippuridaceae. Its position is possibly closer to Araliales (near which it was placed in Engler & Prantl's "Die Natürlichen Pflanzenfamilien") than to Cornales. However, one of us (Thorne) agrees with Orchard in placing Haloragaceae in Cornales, and considers Gunneraceae and Hippuridaceae (see below) as related families in the Haloragineae.

RHIZOPHORACEAE

The homogeneity of Rhizophoraceae needs careful study. Such segregates have been described as Anisophylleaceae and Cassipoureaceae. Rhizophoraceae are trees or shrubs, tanniniferous as in myrtalean families, and with opposite or alternate leaves. The stipules in some mangrove genera (Rhizophoreae) are relatively large and entire, but in another generic group they are minute and even dissected into minute components situated in the leaf axils. Contrary to the Myrtales (except Alzatea), the nodes are trilacunar. The vessel elements in some Rhizophoraceae have scalariform or mixed scalariform/simple perforation plates, which are barely known in Myrtales. The flowers show similarities with those in myrtalean families (those in Macarisia, for example, with flowers as in Lythraceae). They vary from nearly hypogynous or perigynous (e.g., Ceriops) to hemi-epigynous (Rhizophora) or epigynous, and have variable merous conditions, including the tetramerous (cf. Sonneratiaceae). A hypanthium extending beyond the ovary occurs in some genera with epigynous flowers. Also the basically diplostemonous flower type is in agreement with Myrtales; in Kandelia the stamens are numerous (cf. Lagerstroemia in Lythraceae). An intrastaminal nectariferous disc is generally present in the flower (cf. Combretaceae). The pollen grains are tricolporate and comparable to the basic myrtalean type. There are two to six carpels forming a pistil with as many locules (rarely a single locule) and with a simple style. The ovules are bitegmic and crassinucellate although the integuments have more cell layers than is usual in myrtalean families and the nucellus is destroyed much earlier in development (Mauritzon, 1939). The baccate to capsular fruit contains one or few seeds, the seed coat of which Corner (1976) found to resemble that in some myrtalean families as well

as that in Lecythidaceae. The seeds of several genera contain more endosperm than is found in myrtalean families.

Chemically there is hardly any conspicuous feature to distinguish Rhizophoraceae from Myrtales, but the combination of chemical attributes is not unusual. To one of us (Dahlgren) the lack of iridoid compounds and the richness of tannins argue strongly against a position of Rhizophoraceae in the Cornales, which is further supported by the embryological features: bitegmic, crassinucellate ovules, formation of parietal cells, and nuclear endosperm formation. The other of us (Thorne), however, prefers to place Rhizophoraceae in Rhizophorineae, near Haloragineae, in his Cornales (which constitute with Araliales his Corniflorae). He regards Corniflorae as having common ancestry with Rosiflorae and Myrtiflorae, and believes the probable common ancestors of these three superorders as being most nearly represented today by various members of the Saxifragaceae, in the broadest sense.

It is our conclusion that Rhizophoraceae should be excluded from Myrtales, but that they possess (in diverse genera) a combination of features likely to have occurred in pre-myrtalean ancestors, which could well indicate a fairly close common origin.

LECYTHIDACEAE

The family Lecythidaceae (incl. Asteranthaceae, Barringtoniaceae, Foetidiaceae, and Napoleonaceae; Prance & Mori, 1977, 1978) has frequently been placed in Myrtales, alternatives being its inclusion in Theales, as suggested independently by both of the present authors (Dahlgren, 1975a, 1980a; Thorne, 1976, 1981), or its treatment in a separate order (Cronquist, 1968, 1981).

Lecythidaceae are mainly trees, which, contrary to Myrtales, lack internal phloem and vestured pits. The vessels sometimes have scalariform, although more often simple, perforation plates. The leaves are consistently alternate and entire, and in certain genera, at least, are provided with minute stipules; for this last reason and other reasons the family is considered to be myrtalean by Weberling (pers. comm.). Stomata are anisocytic, a condition rather rare in Myrtales (but known within Onagraceae and Melastomataceae). The flowers have variable merous conditions, and are commonly large. They are hemi-epigynous or epigynous, often with con-

nate sepals. The petals are broad and imbricate (rarely lacking). There are generally numerous stamens and staminodia, symmetrically or asymmetrically disposed and developing in centrifugal sequence, as in most Theales. The pollen grains, at least in certain genera, are trinucleate when dispersed, and the tapetum is reported to be amoeboid. In both of these features the family deviates strongly from the myrtalean pattern. The pollen grains are tricolpate, often syncolpate (the Planchonia-type; Erdtman, 1952) or tricolporoidate, whereas, the simply colpate condition is unknown in the Myrtales. The ovary is 2-6-carpellate, with as many locules, and has a simple style. Placentation is axile to basal, and the ovules bitegmic and tenuinucellate, with the integuments being thicker and the nucellus more rapidly destroyed during its development than is the case in myrtalean taxa (Mauritzon, 1939), Axinandra excepted (Tobe & Raven, 1983b). A parietal cell is not formed. In these latter attributes Lecythidaceae are thealean. The fruits are of various kinds and often very large (Prance & Mori, 1978), and also the seeds (as in Bertholletia) are sometimes conspicuously large. The endosperm is chiefly or entirely absorbed during seed development and the embryo is large and rich in fat, as in myrtalean families.

The chemical contents of Lecythidaceae largely agree with those of myrtalean families (see above), but also agree with those in Theales. Lack of internal phloem, relatively more primitive vessels without vestured pitting, presence of wedge-shaped phloem-rays, alternate leaf arrangement, polymerous, centrifugally developing androecium, and tenuinucellate ovules all indicate thealean affinity, as does the lack of endosperm in the ripe seeds. A funicular aril, as found in some Lecythidaceae, has its correspondence in the thealean Clusiaceae. We do not claim, here, that the position of Lecythidaceae in Theales is settled, but a position in that order, especially in its own suborder, seems most appropriate.

ELATINACEAE

The small aquatic family Elatinaceae is generally considered to be thealean, but deviates from most Theales in some features, such as in having stipules and in having crassinucellate ovules.

The family consists of Elatine and Bergia, which are herbaceous, with the exception of the

partly suffrutescent Bergia suffruticosa Fenzl. The leaves are opposite or verticillate and possess small interpetiolar stipules. Neither internal phloem nor vestured pitting has been reported. The small flowers are solitary or aggregated in cymes in the leaf axils and possess six or fewer (sometimes four) sepals and an equal number of petals, and are diplostemonous or haplostemonous. Hypanthial as well as disc structures are lacking. The pollen grains are tricolporate, bi-or trinucleate when dispersed, and the 2-5 carpels form a syncarpous, 2-5-locular ovary with bitegmic, crassinucellate ovules and nuclear endosperm formation. The seeds have little endosperm (see also Tobe & Raven, 1983a), and the embryo varies from nearly straight to strongly curved. It is filled with protein and fat.

This little family exhibits a combination of fairly common attributes which are also found in many Myrtales and Theales. The lack of internal phloem and vestured pitting, the very different interpetiolar stipules, and the hypogynous rather than perigynous flower argue against a position in Myrtales.

CORIDACEAE

The monotypic family Coridaceae recognized by one of us (Dahlgren) is normally considered a comfortable member of Primulales and the single genus, Coris, is most often treated in Primulaceae. Sattler (1962) provoked new ideas in finding similarities between Coris and certain Lythraceae, for example in the differentiation of calyx. The following similarities between Coris and Lythraceae were mentioned by Sattler: (1) descending initiation of the sepal primordia in Coris, occurring also in Cuphea; (2) similar epicalyx-like structures; (3) valvate aestivation of calyx lobes in both groups; (4) strongly convex floral apical meristem in Coris and Cuphea; (5) the centrifugally initiated petals in Coris and in Cuphea, Lythrum, and Ammannia; (6) single antepetalous staminal whorl in Coris and in lythraceous taxa, such as Diplusodon hexander DC.; (7) carpel initiation, starting as an annular ridge in Coris and in Cuphea; (8) strongly reduced septa in the ovary in certain Lythraceae, reminiscent of the condition in Coris, where there is a free central placental column; (9) zygomorphic flowers in Coris and, although weakly, in some Lythraceae; (10) similar pale crimson petal color, and (11) secretorial cavities in Coris and Cuphea

The ovules in Coris are bitegmic and tenuinucellate; in the latter respect they differ from those in Myrtales. In the genera of Lythraceae studied by Joshi and Venkateswarlu (1935a, 1935b, 1936) the ovules are crassinucellate and cut off a parietal cell, although in the smallerflowered genera the nucelli tend to have fewer cells. The condition in Coris is at present being investigated by Bolt-Jørgensen (Copenhagen). It seems that many features of Lythraceae and Coris are held in common, and at the present point it not easy to establish whether these have mostly evolved by convergence, so that we can reject Airy-Shaw's and Sattler's hypothesis of an affinity. The overall pattern of placentation and embryology in Coris is primulaceous. Species of Nesaea in Lythraceae (Fernandes, 1978, 1980) are superficially quite similar to Coris.

Among the differences between *Coris* and Lythraceae thus remaining to be explained are the alternate exstipulate leaves, the lack of internal phloem, the wholly free-central placentation, and the tenuinucellate ovules of *Coris*, all non-myrtalean features.

Thus both of the authors reject (Thorne strongly so) placement of Coris in Myrtales.

CHRYSOBALANACEAE

The members of this family have alternate, simple, entire, and stipulate leaves, the stipules being small but not as minute as in myrtalean families. The stems lack internal phloem (Prance, pers. comm.) and vestured pits in the vessel elements. In flower construction Chrysobalanaceae show conspicuous similarities to myrtalean families, being, for example, perigynous with a frequently conspicuous hypanthium, on the rim of which sepals, (often small) petals, and stamens are inserted. The perianth whorls are 5-merous. Stamen number is variable, although a diplostemonous basic condition (as in Licania), is probable, from which secondarily oligo- and multistaminate conditions have evolved. When numerous, the stamens may be united in groups. The pollen grains are 3-colporate. Arguments against considering Chrysobalanaceae as rosaceous, are, for example, the occurrence of foliar sclereids and the syncarpous (although gynobasic and generally pseudomonomerous) character of the gynoecium when this is 2- or 3-carpellate. A reduction of carpel number to one (i.e., a secondary, truly monomerous condition) no doubt also occurs in part of the family (cf. the discussion under Elaeagnaceae). The embryology of the family is very similar to that in families of Theales (Tobe & Raven, 1984d), which favors inclusion of Chrysobalanaceae in that order.

Chrysobalanaceae contain ellagic acid and ellagi-tannins (Hegnauer, 1973) as do Myrtales (and some Theales and Rosaceae, but not Amygdalaceae or Malaceae). The embryo contains protein and fat, rarely (*Couepia*) some starch. In these features the family agrees with Myrtales.

In the light of the several conspicuous differences between Chrysobalanaceae and Rosales sensu stricto and similarities between Chrysobalanaceae and, for example, Ochnaceae of Theales, the family should not be considered as the link between Rosales and Myrtales as may be thought from some gross morphological features. Should there prove to be a connection between the Myrtales and the Theales (see p. 688), then Chrysobalanaceae come into the picture.

ELAEAGNACEAE

Elaeagnaceae have occasionally, but rather rarely of late, been associated with Myrtales. Some vegetative features argue against a myrtalean relationship, as the alternate exstipulate leaves, lack of internal phloem, and lack of vestured pitting in the vessel elements. The anomocytic stomata and peltate hairs are found also in Combretaceae of Myrtales, and the vessel elements have simple perforation plates as in Myrtales. The flowers, which are mostly unisexual, agree in several respects with those in Myrtales, being often tetramerous, the male flowers being haplo- or diplostemonous, and at least the female flowers being provided with a hypanthium. Petals are missing. Foreign to Myrtales is the monocarpellate pistil with a single erect ovule, but embryological features and the exendospermous seed of Elaeagnaceae agree well with the conditions in Myrtales. Chemically Elaeagnaceae agree also fairly well with Myrtales (p. 661), although their alkaloid contents, tryptophane derivatives, are special.

Eyde (1975) considers that Elaeagnaceae cannot be derived from Myrtales as it has a truly solitary carpel (which is evidently the case; Eyde, 1975, fig. 2), but we see no reason why the carpel number could not be reduced in a syncarpous as well as in an apocarpous gynoecium. However, there are other reasons why Elaeagnaceae cannot be considered of myrtalean origin, such as their lack of internal phloem. The pollen grains are tricolporate, being sometimes reminiscent of those in certain Myrtaceae.

Both authors (Thorne, 1981; Dahlgren, 1980a) believe that Elaeagnaceae are closely related to Rhamnaceae, which was also proposed by Hutchinson (1959). This is supported by similarity of seed coat (Corner, 1976) and by parasitizing fungi (Thorne, 1979). The position of both of these families in relation to the Myrtales is assumed to be distant, with some similarities explained by convergence (see Rhamnaceae, below), but these similarities clearly deserve further study.

FAMILIES SOMETIMES ASSOCIATED WITH, BUT APPARENTLY DISTANTLY RELATED TO MYRTALES

Rhamnaceae are among those families which only occasionally have been mentioned as possibly related to myrtalean families, but which exhibit some interesting similarities. They are woody and have simple, often opposite leaves with (or rarely without) small or moderate-sized stipules, which may be present as a row of small hair-like structures. Intraxylary phloem is lacking, and the vessels have no vestured pitting although their perforation plates are simple as in Myrtales. The flowers are actinomorphic, with inferior to superior ovary, and generally have small petals opposite a single whorl of stamens. A hypanthium occurs in several genera (cf. Elaeagnaceae), and there is usually a prominent disc. The pollen grains are mostly tricolporate and two-celled. The carpels are 2-5, forming a syncarpous 2-5-locular pistil with simple style, which agrees with myrtalean families, although the locules have but one ovule each. The embryology is largely as in Myrtales and the seeds have little endosperm and a relatively large, straight embryo. Chemically, the Rhamnaceae are peculiar in the production of benzylisoquinoline alkaloids, documented in several genera. Anthraquinones are common. Tannins are present, but ellagic acid or ellagi-tannins have not been recorded.

The family cannot be considered seriously for membership in Myrtales, especially because of vegetative anatomy and chemistry, although technically there are a number of obvious similarities.

Datiscaceae were recently thoroughly reviewed by Davidson (1973, 1976). Shaw (1973) suggested relationship with Haloragaceae, which are often placed in Myrtales. Therefore mention may be justified here. Datiscaceae consist of three genera, the herbaceous Datisca and the tree genera Octomeles and Tetrameles. The latter genera may represent the more nearly ancestral forms. Internal phloem is lacking in the stem. The leaves are alternate and exstipulate and bear multiseriate, peltate or glandular hairs. As in many Myrtales, these genera possess branched sclereid idioblasts. The flowers are 4- to 8-merous in calyx and (when present) corolla, and the pollen grains are 3-colporate. The stylodia are separate, not fused into a single style as in the Myrtales, and the placentation is parietal (to nearly central), which is rare in Myrtales. Davidson on the basis of an extensive survey of the family concluded that it was not allied to the Myrtales. Links to Flacourtiaceae and other families of Violales are apparently most likely.

Marcgraviaceae in their opposite leaves, flowers which may have numerous stamens, and the nearly exendospermous seeds show some superficial similarity to Myrtales. There is no internal phloem, no vestured pitting, stipules are lacking, androecial developmental sequence is centrifugal, and ovules are tenuinucellate and at least in some taxa have cellular endosperm formation. These features are all lacking in Myrtales (cellular endosperm also in Theales). From the evidence available Marcgraviaceae seem best placed in Theales.

Theaceae, as a representative family of the Theales, have some superficial similarities to myrtalean families. The leaves are simple and, as in several families of Myrtales, often are well supplied with branched sclereid idioblasts. Stipules, internal phloem, and vestured pitting are lacking. The flowers are mostly more open than in the Myrtales and lack the conspicuous hypanthium of this order. They have from five (Pelliceria and other genera) to numerous stamens. These, however, tend to develop in centrifugal succession. The anthers of a Camellia species, for example, also possess a laterally expanded connective reminiscent of that in some myrtalean members. The syncarpous pistil has a single style, and the ovules are anatropous and, with the exception of their tenuinucellate character (and lack of development of parietal cell), are somewhat similar in their embryology to those of Myrtales. Rarely are they unitegmic. The seeds also lack endosperm. The alkaloid content in many Theaceae consists of purin bases. Otherwise Theaceae resemble the myrtalean families in containing ellagi-tannins. The similarities between Theaceae (and other thealean families) and Myrtales are ambiguous but (in the view especially of one of us, Thorne) do not indicate a close phylogenetic affinity at all.

Clusiaceae (Hypericaceae) agree with Theaceae in showing certain similarities to Myrtales (see also above for Lecythidaceae), but do not have the internal phloem and usually lack stipules. The lack of hypanthium, the tenuinucellate ovules, and the frequent occurrence of an aril indicate strongly thealean rather than myrtalean affinity. In the schizogenous secretory ducts and the occurrence of branched sclereid idioblasts they may superficially resemble Myrtaceae, but the secretory ducts contain great amounts of yellow to red phenolic pigments consisting of anthraquinone and xanthone derivatives and coumarins, which are not matched in Myrtaceae. A close relationship to Myrtales thus cannot be seriously proposed.

Myrsinaceae consist of woody plants with alternate or opposite leaves without stipules. Internal phloem is lacking. The vegetative parts have schizogenous ducts with resinous contents. In contrast to Myrtales there is no hypanthium, although the corolla is more or less sympetalous. The stamens, in one whorl, are antepetalous, a condition rarely met with in Myrtales (but present for example in Lythraceae). The free-central placenta is not indicative of myrtalean affinity either, and the ovules in addition are tenuinucellate. Finally, the seeds are rich in endosperm, which they are not in Myrtales. These conditions indicate that Myrsinaceae are rather closely allied to Primulaceae rather than to families in Myrtales.

Geissolomataceae (see Dahlgren & Rao, 1969; Carlquist, 1975) are a monotypic South African family which has often been associated with Penaeaceae of Myrtales. It has opposite leaves with minute stipular teeth. The flowers have four basally connate sepals, a diplostemonous androecium and four carpels, which may suggest myrtalean affinity. However, internal phloem is lacking and the vessels lack vestured pitting and have scalariform perforation plates with numerous bars (indeed, there may hardly be perforations at all, see Fagerlind & Dunbar, 1973). In addition, the pollen grains lack pseudocolpi (which Penaeaceae have), the stylodial branches

are free from each other, and the seeds have copious endosperm and a small embryo. Therefore, there are no reasons at all to include the genus in Myrtales. Rather, a position in or near Hamamelidales or in Cunoniales (proposed by Dahlgren) seems appropriate, which agrees well with the view of Thorne, who firmly believes that Geissolomataceae are closely related to Bruniaceae and places these in the suborder Brunineae, along with Buxineae and Pittosporineae, in a widely circumscribed order, Pittosporales (Carlquist, 1975; Thorne, 1975, 1977, 1981).

Gunneraceae, with the single genus Gunnera, are herbaceous plants with a habit different from most Myrtales. The larger, lateral stipules, reduced flowers, separate, long stylodial branches, cellular endosperm formation, and seed with copious endosperm and a tiny embryo, comprise important differences from Myrtales. This family also seems to have no close relationship to Haloragaceae, though one of us (Thorne) still prefers to retain Gunneraceae in his suborder Haloragineae of Cornales.

Proteaceae show certain superficial similarities to myrtalean families but lack internal phloem and have alternate leaves without stipules. The flowers are hypo- to perigynous and as in most Myrtales have a tetramerous perianth on a conspicuous hypanthium. Pollen grains morphologically have some resemblance to those in Onagraceae (but no viscin threads and a very different exine structure) but hardly to those in other myrtalean families. The pistil is monocarpellate. The embryology agrees with that of Myrtales in most features, and the ripe seed is almost devoid of endosperm. The chemical characters are similar to those of Myrtales (tannins, flavonols, occasional aluminum accumulation, cyanogenic compounds) except that ellagic acid is not recorded. Proteales are quite distinct from Myr-

Malpighiaceae resemble superficially Lythraceae in the often violet, unguiculate petals with wavy margins. They lack internal phloem, but the vessels have vestured pits as in Myrtales and the perforation plates are simple. The leaves are simple, alternate or more often opposite, and may or may not have stipules. The paracytic stomata and branched "malpighian" hairs would be, however, unusual in Myrtales, and papillae are frequently present on the lower surface of the leaves. The plane of symmetry of the flower, which is slightly zygomorphic, is oblique, the flowers are obdiplostemonous, and in contrast

to all Myrtales, the stylodial branches are often separate to their base. Each of the 3–5 locules has one pendulous, hemi-anatropous ovule with an embryology similar to that of Myrtales; the embryo sac, at least in some cases, is tetrasporic and reputed to resemble that in Penaeaceae. The seeds are exendospermous. The fruits vary but tend to be schizocarps, quite dissimilar to any found in Myrtales. Chemically, the family resembles various Myrtales in having triterpene saponins, but ellagic acid is not reported and the tannins seem to be of the condensed type only.

Malpighiaceae do not seem to be very close to Myrtales, but a number of similarities suggest that a set of attributes occurring in Polygalales (or Polygalineae of Geraniales) are held in common with that in Myrtales.

Pittosporaceae lack stipules and have schizogenous secretory ducts with resinous contents. Their production of polyacetylenes, unitegmic, tenuinucellate ovules, and copious endosperm and very small embryo in the ripe seeds do not indicate myrtalean affinity.

Escalloniaceae and Icacinaceae, whether closely related to each other or not, both differ from Myrtales in similar ways. They lack stipules and a hypanthium, and they have unitegmic and sometimes tenuinucellate ovules with cellular endosperm formation. In addition, they occasionally contain iridoids, which have not been found in Myrtales.

Montiniaceae (Montinia, Grevea, and Kaliphora) agree in morphology and especially in embryology with the majority of Cornales and also contain iridoids, which are quite common in this order. Griseliniaceae are probably related here too, along with Escalloniaceae, but need to be studied further.

Columelliaceae in overall floral construction and embryology (unitegmic, tenuinucellate ovules with cellular endosperm formation and terminal endosperm haustoria) are typically cornalean and thus can safely be excluded from Myrtales.

Montinioideae, Griselinioideae, Escalloniaceae, and Columellaceae are treated by one of us (Thorne) in the Saxifragineae of the order Rosales, which he considers to have common origin with the Cornales.

Dialypetalanthaceae (Fig. 16), like Rubiaceae, have opposite leaves with interpetiolar stipules, but the petals are free, the stamens 8–12(–16), the ovules more numerous, and the seeds different. The pistil is bicarpellate, and the fruit, although capsule-like, opens up as a schizocarp.

The flat seeds are numerous, flat, winged, and apparently have evolved from unitegmic ovules. The position of this family although not yet firmly placed in Gentianales certainly does not seem to fit into Myrtales. The stomata (H. Rasmussen, pers. comm.) are paracytic, indicating (albeit not definitively) affinity with the Rubiaceae. *Dialypetalanthus* is probably an aberrant early off-shoot of the Rubiaceae or a relict family closely related to the Rubiaceae in the Gentianales.

Loganiaceae and Rubiaceae are preferably placed in the same order, Gentianales, of sympetalous angiosperms. Like Myrtales they have opposite leaves, vestured pits, and many Loganiaceae also have bicollateral vascular bundles. Interpetiolar stipules of rubiaceous type are absent in typical Myrtales, and stipules are lacking in Loganiaceae.

Loganiaceae and several other families in Gentianales show a combination of intraxylary phloem and vestured pits, as do Myrtales, Thymelaeaceae (or most of its taxa according to its circumscription), part of Vochysiaceae, and one genus of Polygonaceae. Van Vliet and Baas (1984) stress the common occurrence in Myrtales and Gentianales, e.g., Loganiaceae sensu lato, of the combination of intraxylary phloem, vestured pits, fiber-tracheids, and diversity of crystal types (including raphides and styloids) as shown by Mennega (1980). This calls for a general survey of other features. The embryology of Loganiaceae [which in the sense of Leeuwenberg and Leenhouts (1980) is probably heterogeneous!] is characterized by unitegmic, tenuinucellate ovules with nuclear or rarely cellular endosperm formation (Dahlgren, 1975b). The seeds are also generally provided with copious endosperm. Chemically, Gentianales show little affinity with Myrtales (see Dahlgren et al., 1981), and in floral morphology the similarity may be superficial. Thus, in spite of the fact that Myrtales and Gentianales are adjacent in the diagram of Dahlgren (1980a; Dahlgren et al., 1981), one of us (Dahlgren) does not consider the two orders as closely allied. Rather, he thinks in this case that it is likely that the wood-anatomical similarities have evolved by convergence. This is probably also the case, independently, with Thymelaeaceae. The other author (Thorne) believes that these wood-anatomical and floral similarities may have been retained from common, proto-rosalean

ancestors.

Hippuridaceae (= Hippuris) from Hegnauer's (1969) chemical account, also according to Dahl-

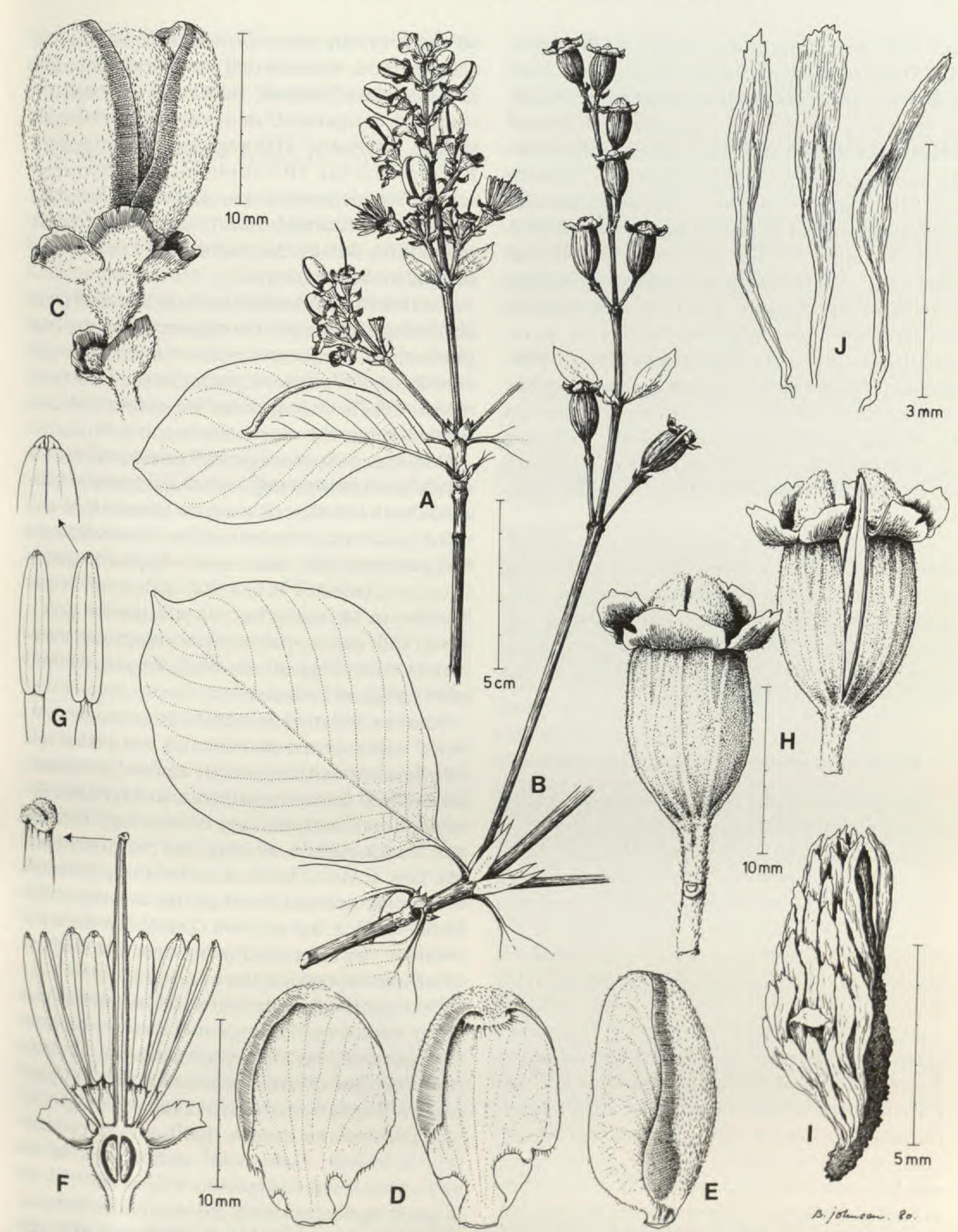


FIGURE 16. Dialypetalanthus fuscescens Kuhlm., forming the monotypic Brazilian Dialypetalanthaceae: A-G. Prance et al. 8967; H-J. Prance et al. 6526.—A. most part of inflorescence and upper leaf pairs of branch.—B. fruiting branch, note the variation of stipule size in successive leaves.—C. flower just before opening, showing decussate sepals and petals.—D. inner petals.—E. an outer petal.—F. flower in longitudinal section, petals removed; above: stigma in detail.—G. stamens; above: staminal tip in detail.—H. capsules in different views, the right opening along carpel commissures.—I. placenta with seeds.—J. seeds. (Orig., del. B. Johnsen.)

gren (1975a), Jensen et al. (1975), and Wagenitz (1975), seem to be best removed far from Haloragaceae, and show no discernible relationships to Myrtales either. Yet Cronquist (1968) and Thorne (1976, 1981) on the basis of other similarities prefer to retain Hippuridaceae in the same order Haloragales or suborder, Haloragineae, with the Haloragaceae and Gunneraceae, though both agree that these families are not close relatives of Myrtales but probably have common ancestry with them and Rosales. The leaves are verticillate, and the small, epigynous flowers are so reduced as to give very little morphological indication of relationships. However, the unitegmic, tenuinucellate ovules with cellular endosperm formation, and the chemical spectrum, including the biosynthesis of carbocyclic iridoids, indicate scrophularialean or, alternately, cornalean affinity.

Callitrichaceae have now received an acceptable position near Verbenaceae and Lamiaceae on the basis of the 4-seeded schizocarps, unitegmic and tenuinucellate ovules, cellular endosperm formation, terminal endosperm haustoria, and carbocyclic iridoids, all characteristics that are foreign to Myrtales.

RELATIONSHIPS OF THE ORDER MYRTALES

The position of the order Myrtales has varied in different classifications and is still a matter of divergent opinions. Cronquist (1981) and Takhtajan (1980) in their recent classifications have been somewhat constrained by their division into the subclasses Dilleniidae and Rosidae of the majority of choripetalous orders of dicotyledons. Myrtales in both classifications are placed in the Rosidae, where they form the main order in Takhtajan's superorder Myrtanae. It is generally agreed that the order is more or less related to Rosiflorae, including Rosales, Saxifragales, and Cunoniales, although other, quite small, orders occasionally treated with Myrtanae are considered even more closely related, as Haloragales and Rhizophorales (and Lecythidales) when these are acknowledged. Other orders sometimes recognized and often associated with Myrtales are Elaeagnales and Thymelaeales. Theales and presumably closely related Primulales, being members of their Dilleniidae, have tended to be left out of comparison, although at one occasion or another the similarity has been pointed out, e.g., by Hickey and Wolfe (1975).

Several of these groups have been compared

on the previous pages with myrtalean families, notably those representing monofamilial orders in some classifications, or have even been included as components in a more widely circumscribed Myrtales: Haloragaceae (Haloragales), Rhizophoraceae (Rhizophorales), Thymelaeaceae (Thymelaeales), Lecythidaceae (Lecythidales), and Elaeagnaceae (Elaeagnales). Some generalities will be discussed, and other orders compared with Myrtales.

Two attributes to which we have attached great importance above are the occurrence of internal phloem, i.e., the presence of bicollateral vascular strands, and of vestured pitting in the vessel elements. When the Myrtales are strictly circumscribed, these characteristics become critical.

Only one of the serious candidate families for myrtalean membership mentioned above possesses both bicollateral vascular strands and vestured pits, viz., Thymelaeaceae (these features being shared also with some Euphorbiaceae). Cronquist (1968, 1981, 1984) includes Thymelaeaceae in Myrtales, but, as pointed out previously, this meets with serious objections, especially with regard to phytochemical and embryological evidence.

Another order where opposite leaves are combined with internal phloem and vestured pits is Gentianales, within which especially Loganiaceae show some resemblance to Myrtales. Because floral morphology, embryology (unitegmic, tenuinucellate ovules), and chemistry (lack of ellagic acid and tannins on the whole, presence of iridoids and indole alkaloids) are vastly different, one of the authors (Dahlgren) does not consider the relationship between the Loganiaceae and Myrtales to be at all close.

Disregarding bicollateral vascular strands and vestured pitting, Haloragaceae, Rhizophoraceae, Elaeagnaceae, and Chrysobalanaceae provide combinations of attributes which are not seriously different from the myrtalean, although various peculiarities in each family would be aberrant or at least "untypical" in Myrtales. In the main phytochemical spectrum these families are in good agreement with the myrtalean pattern, and vegetative as well as floral details, also, are conspicuously similar in various respects. However, it is important to remember that most of the basic features of Myrtales are widespread in choripetalous dicotyledons. None of the families mentioned which lack internal phloem and vestured pitting seems to relate (in comparativemorphological terms) clearly to any of the "core

families" of Myrtales. Thus it seems convenient and adequate to use the presence of these two attributes as significant diagnostic criteria for Myrtales.

MYRTALEAN VERSUS ROSALEAN ATTRIBUTES

One of the families mentioned above as particularly similar to many Myrtales is Chrysobalanaceae. This has been alternately referred to Rosales and Fabales (where these orders are not united); whereas, its position in Myrtales has hardly ever been suggested. Disregarding the lack of internal phloem and vestured pitting, the family seems to agree nearly as well with myrtalean as with rosalean attributes, thus justifying a comparison. Rosales sensu stricto normally include at least Rosaceae, Neuradaceae, Amygdalaceae, and Malaceae [all more often treated as subfamilies of Rosaceae sensu lato, whereas the Chrysobalanaceae are often treated separately, in the vicinity of Sapindaceae and Connaraceae (in Sapindales or Sapindineae of Rutales)].

Vegetatively Rosales sensu stricto are diversified: they are basically woody plants, the vessels of which generally have simple perforation plates. Stomata are mostly anomocytic, mucilage cells are common, and glandular hairs are common. The leaves are generally alternate, quite often compound, and in many species have well-developed stipules (never represented by rows of finger-like projections in the leaf axils as in many Myrtales). The leaf teeth in Rosales are of the Rosoid type (Hickey & Wolfe, 1975) and are slightly resembled by those in some genera of Onagraceae (Hickey, pers. comm.). The flowers are basically actinomorphic and the inflorescence determinate. A conspicuous similarity to the Myrtales is the prominently developed floral receptacle, which in several groups results in perigynous, urceolate types comparable to those in many Myrtales. A second trend, with elevated receptacle, has not evolved in the Myrtales. The tetramerous condition is rare in Rosales, but common (although, quite likely, secondary) in the Myrtales. The androecium of Rosales, although probably evolved from a diplostemonous basic type, has multiplied by the insertion of more whorls as well as by increase of initials in each whorl. A presumed primitive condition is the apocarpy of many Rosales. A syncarpous pistil occurs only in a few Chrysobalanaceae and in epigynous Malaceae (= Rosaceae subfam. Maloideae). Rosales sensu stricto and Myrtales agree essentially in pollen morphology, embryology,

sparsity of endosperm in seed, and also in phytochemistry. Chrysobalanaceae deviate from the "typical" rosaceous pattern in several respects. In some of these, as syncarpy, single style, urceolate receptacle, and mode of stamen multiplication, they approach the Myrtales, although this may be by convergence. New embryological evidence (Tobe & Raven, 1984d) indicates great agreement with families of Theales, and Chrysobalanaceae may best be treated as a member of this order.

MYRTALEAN VERSUS CUNONIALEAN ATTRIBUTES

Cunoniales (Dahlgren, 1980a) can be variously circumscribed, but their delimitation from Saxifragales contributes difficulties. In some respects this group of families is more specialized than Rosales sensu stricto, e.g., in having more often syncarpous pistils, but in other features it shows much less specialization, as in wood-anatomical characteristics and abundance of endosperm in the seed. Stipules with various degrees of development occur in the order, thus agreeing with Myrtales, where they are mostly present but minute. The basically diplostemonous flowers, which are more often 5- than 4-merous, the general lack of a hypanthium, and the common presence of a well-developed disc are only partly in agreement with the myrtalean pattern. The gynoecium in Cunoniales ranges from nearly apocarpous to syncarpous, and the mature seeds differ from those in Myrtales by having, as a rule, copious endosperm, but embryological and phytochemical characteristics are not very different from those in Myrtales. As Cunoniales, which are dubiously homogeneous, show resemblance to Rosales and Saxifragales (Thorne treats all three as suborders of Rosales), they also approach a hypothetical ancestral myrtalean type. However, the similarity between families of the orders is not particularly impressive to some phylogenists.

MYRTALEAN VERSUS SAXIFRAGALEAN ATTRIBUTES

Saxifragales sensu stricto (Dahlgren, 1980a), include Crassulaceae, Saxifragaceae sensu stricto, and a few small families, e.g., Grossulariaceae (Saxifragaceae subfam. Ribesioideae), some often included in Saxifraceaeae sensu lato. The two principal families may not be as closely allied to each other as often stated. Each of them agrees in many respects with Myrtales, especially in floral construction and partly also in chemistry. Op-

posite leaves characterize many Crassulaceae, but stipules are lacking. The pentamerous or, especially in Crassulaceae, often tetramerous flowers are obdiplostemonous, but the significance of the difference between this and the diplostemonous condition is obscure. In Crassulaceae, the carpels are isomerous with the other floral whorls, as in many Myrtales, and the seeds are also exendospermous; whereas, in Saxifragaceae the seeds have copious endosperm. The tubular flowers of many Crassulaceae, e.g., Kalanchoë, should not be confused with the similar ones in many Myrtales, because in Myrtales the floral tube represents a true hypanthium. In Crassulaceae, however, it consists of the fused petals only (sympetaly!), to which the filaments are more or less adnate. The endosperm formation in Saxifragales is intermediate (helobial) or cellular, which is never the case in Myrtales.

In Saxifragales, the Grossulariaceae (*Ribes*), no doubt by a combination of parallel and convergent evolution, have developed a number of fascinating similarities to *Fuchsia* (Onagraceae), and exhibit a combination of epigyny, a simple (or cleft) style, an urceolate to tubular hypanthium, often brightly colored like the calyx lobes, frequently reduced petals, and a baccate fruit (*Ribes speciosum* is called "California-Fuchsia"). The seeds are, however, enclosed by a carnose, juicy arillus, the endosperm is copious, and the embryo is minute.

There are accordingly no close bonds between the Saxifragales sensu stricto and the Myrtales, although some basic features indicate that the groups may be derived from distant common ancestors.

MYRTALEAN VERSUS RUTIFLOREAN ATTRIBUTES

What has been said for the previous orders is partly valid also for various members of the orders Rutales sensu stricto, Sapindales, Geraniales, and Polygalales, where the general level of organization based on a pentacyclic, either diplostemonous or obdiplostemonous, floral plan partly corresponds to that in Myrtales. Odd families, such as Malpighiaceae and Erythroxylaceae, may strongly resemble myrtalean families but each exhibits important differences from them and lacks internal phloem and a hypanthium. In both aforementioned families there are, for example, separate stylodial branches instead of a single style. There is, however, within the ruti-

florean complex a basic morphological, embryological, and phytochemical pattern of characteristics which approaches that of the Rosiflorae as well as the Myrtiflorae. However, any relationships between these groups must be fairly distant.

MYRTALEAN VERSUS THEALEAN ATTRIBUTES

The comparison between the orders Myrtales and Theales is justified because of certain shared attributes. Also, Lecythidaceae have quite often been included in Myrtales, and indeed some of their members are similar to such large-flowered, polyandrous tree genera as Sonneratia, Duabanga, Punica, and Lafoënsia within Myrtales. Also various details, such as the occurrence of minute stipules in some Lecythidaceae (Weberling, 1958) and the similar phytochemistry, could be taken to support the view that the Theales and Myrtales may be distantly related.

The members of Theales are mostly woody. They lack the internal phloem and vestured pitting of the Myrtales and often have more primitive vessel types; but they resemble many Myrtales frequently in having foliar sclereids, although possession of the latter is usually a feature of low phylogenetic significance at this level (Rao & Das, 1979). The flowers vary in merous conditions but are more rarely tetramerous and a typical hypanthium is rare. The petals are normally broad and imbricate. Typical of a great part of Theales are the numerous stamens with centrifugal developmental succession. Pollen morphology (see above, under Lecythidaceae), bitegmic ovules, nuclear endosperm formation, and sparsity or lack of endosperm in the ripe seed are in some, but not high level, agreement with conditions in Myrtales, but the ovules are generally tenuinucellate and dissimilar to those in Myrtales. In phytochemical characteristics the two orders are basically similar. Assuming that the numerous stamens are secondary to a diplostemonous state and that the tenuinucellate ovules are derived from crassinucellate ones, the distant ancestors of Theales should approach those of the Myrtales. Many taxonomists, on the basis of the clear differences mentioned, consider the orders very distant, which is reflected in the fact that they are placed in different subclasses, Theales in the Dilleniidae and Myrtales in the Rosidae in the classifications of Takhtajan (1980) and Cron-

quist (1981).

MYRTALEAN VERSUS CORNALEAN ATTRIBUTES

For Rhizophoraceae as well as Haloragaceae, alternative positions suggested in most literature are either in Myrtales or in Cornales. Therefore a short note on the differences between these two orders is justified. Crucial in this connection is the definition and circumscription of Cornales (see Huber, 1963). As defined by one of us (Dahlgren) Cornales include a number of families (among others, Cornaceae, Hydrangeaceae, Montiniaceae, Escalloniaceae, Icacinaceae, Symplocaceae, Adoxaceae, Sambucaceae), with variably opposite or alternate leaves, without internal phloem, with vessel elements having simple or scalariform perforation plates, and lacking vestured pitting. The flowers are sympetalous, and embryologically the families are fairly well defined by the generally unitegmic, tenuinucellate ovules and cellular endosperm formation (Philipson, 1974; Dahlgren, 1975b), which combine with the frequent occurrence of iridoid compounds (Jensen et al., 1975) but lack of ellagitannins. When so circumscribed, Dahlgren considers the order fairly homogeneous, and as having a quite distant relationship with the Myrtales.

In at least the wood-anatomical features, Haloragaceae and Rhizophoraceae agree better with Cornales than with Myrtales, but in other characteristics Dahlgren finds little to support such a relationship.

The second author, Thorne, gives a very different circumscription and definition for his Cornales, which permits inclusion of the abovementioned two families in the order.

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